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The development and use of segregating inbred lines

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THE DEVELOPMENT AND USE OF SEGREGATING INBRED LINES

by

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TABLE OF CONTENTS

INTRODUCTION

In the fowl, plumage colors and morphological traits were first investigated for Mendelian behavior since they were readily classified. However the underlying gene action or hereditary control of the apparently simple traits must entail much more complicated processes. Also such genes may have manifold effects influencing quantitative traits. Accordingly there has been a renewed interest in the effects of several morphological genes in the domestic fowl.

Since gene action involves processes of a biochemical basis, the study of differences produced by a single gene require that the total genotypes to be compared should be as nearly alike as possible. They should be comparable in total genetic sense so that differences ascribed to a single gene under examination are not the joint consequences of it together with numerous unrecognizable factors which different lines normally differ. Such comparability can best be assured within an inbred line.

The segregating inbred lines used in this study were developed by outcrossing an already established inbred line, to bring in a desired gene, and backcrossing the heterozygote in successive generations. Under this procedure some interactions of other factors could possibly obscure differences between heterozygotes and homozygotes of the gene under study. A new character could arise from the homozygosis of a gene

which was heterozygous in the source stock and unlinked to the one selected. This possibility becomes relatively small as the number of backcrosses increases. Linked genes could also pose another problem. The probability of the inclusion of such genes is necessarily higher and would be extremely high if the linkage were very close.

The study of plumage colors and morphological traits has practical considerations as well as fundamental genetic aspects. The introduction of a particular gene into a stock could reduce the economic value of such a line or breed even if the primary effect of the gene would be desirable. For example, the introduction of dominant white into a stock to produce the necessary white bird the market demands can result in significant growth depression (Jaap and Grimes 1956).

With respect to fundamental genetics, segregating inbred lines are of interest in studies of dominance and epistasis. No direct inference of dominance is possible without a valid comparison of the heterozygote with both of the corresponding homozygotes. Not only single contrasts can be examined but the specific interaction of two or more factors could be exhibited.

The present study is concerned with three recognized single gene effects in the domestic fowl: dominant white, rose comb and sex-linked barring.

The objectives of this study are:

(1) To examine dominance relationships of the three genotypes of a single gene in different genetic backgrounds.

(2) To study the possible effects of a single gene on economically important traits in several genetic backgrounds.

REVIEW OF LITERATURE

Dominance

R. A. Fisher (1930) developed a phylogenetic and statistical theory of dominance of wild type over mutations involving a selection of modifiers that shift the phenotype of the heterozygote mutant toward the wild type. His reason was that wild type has a selective advantage which also is conferred upon heterozygotes of the frequently produced mutant. Fisher (1934, 1935, 1938) noted most mutants in the domestic fowl were of the dominant form in contrast to those of Drosophila. The fowl, therefore, provided material to test a crucial point in the dominance theory. If "domestic" dominants had evolved through artificial selection during the process of domestication, this could be demonstrated by showing that in wild stocks not previously subjected to artificial selection, dominance is absent, i.e., the heterozygote is intermediate between two homozygous types.

Fisher's experiment consisted of introducing various genes, thought to be dominants, into a stock of wild jungle fowl. This was done by backcrossing the heterozygote five successive generations to the jungle fowl stock followed by interbreeding the heterozygotes. Thus, all three genotypes of the mutant were obtained in a relatively pure jungle fowl genetic background.

Dominance was found to be incomplete in the case of three

mutants which influenced pigmentation. These were barring, pile (dominant white) and black internal pigment. Barring proved to be more nearly recessive than dominant.

Four other mutants influencing morphological traits were studied: crest, rose comb, polydactyly and feathered shanks. With the exception of crest these mutants did not exhibit clear cut results. However, crest homozygotes manifested cerebral hernia at hatching. This demonstrated a lethal form of crest in the wild jungle fowl stock.

In Drosophila, Blanc (1946) presented evidence of the effect of dominance modifiers "dominigenes" on the action of the gene vestigial (vg) and its alleles. Three main dominigenes were present; one on the X chromosome and one each on the second and third chromosomes. In the presence of both autosomal dominigenes in homozygous condition and the sex-linked dominigene in simplex condition in males and duplex condition in females, almost all flies heterozygous for vestigial (vg) showed scalloping or notching of the distal margin of the wings. This phenotype would be comparable to that characteristic of the lesser vestigial allele, vestigial notched (vg^{no}). In the absence of the sex-linked gene, the autosomal dominigenes together produced only one or two percent notched flies. The dominigenes had no visible effects other than their influence on the dominance of vestigial (vg) except for a possible effect on viability.

Working with cotton Harland (1933) transferred the mutant, crinkled, found in G. barbadense into normal G. hirsutum. After the sixth backcross to hirsutum in two varieties, Harland was unable to classify plants into normal and heterozygous crinkled types. This revealed complete or nearly complete dominance of hirsutum to the crinkled type. The point of view emphasized by Fisher -- that dominance is a function of the genotype as a whole -- is substantiated. However, the crinkled mutant had not previously occurred in hirsutum, and the results do not support the attainment of dominance by the reaction of a species to the repeated occurrence of a mutant.

In the work of Castle (1940), who studied the hooded pattern in rats, modifiers seemed to be of importance. Crosses between hooded and non-hooded gave non-hooded progeny in the F_1 and a 3:1 ratio of non-hooded to hooded in the F_2. Selection for high and low pigment areas in the coat resulted in the high line becoming so dark that only the ventral surface of the body was white, while the low line became so light that only the head and tail were pigmented. The hooded gene itself was not involved, for crossing both the high and the low lines with a wild type rat produced hooded individuals as recessives in the F_2.

McNutt (1954) studied the incidence of ventral tubercles on the sixth cervical vertebrae in four strains of mice.

These were bred with planned heterozygosis for the short-ear gene. His experiment illustrated a variable dominance effect. The short-ear gene pleiotropically suppressed the development of ventral tubercles. The amount of suppression varied with the strains of mice, which indicated the presence of different modifying factors in the genetic background of each strain. Some of these genes were considered as dominance modifiers because the ventral tubercles developed as an irregular dominant character in one strain of mice, but as a recessive in a second strain. Two other strains were intermediate in expression between those discussed here.

Influence of Single Genes on Quantitative Traits

A single gene that governs primarily a morphological trait may influence the performance of quantitative traits if such genes are pleiotropic or if the genes for both characters are linked.

Linkages may exist unbroken over several generations even when a gene is introduced into a pure line and the progeny carrying it are repeatedly backcrossed to the pure line. Bartlett (1935) pointed out that the mean genetical length of a non-terminal chromosomal segment introduced along with gene (A) in a backcross is:

$$\frac{1 - 2^{-n}}{n},$$

where: n is the number of backcrosses. This value

approximates to $\frac{1}{n}$ when n is large.

Queen (1931) demonstrated that size and color in mice were linked. An analysis of his data indicated an association between large size and the recessive character, brown coat color.

Lindstrom (1929) reported that the number of rows in the maize ear, a quantitative character, was probably linked to such qualitative characters as cob, aleurone and endosperm color, as well as to endosperm texture (sugary). In tomatoes, Lindstrom (1926) presented evidence that the genes for color, yellow (Y) and red (R), were linked with major size factors.

Grüneburg (1938) theorized that pleiotropy can arise in three different ways. (1) Two effects, A and B may be produced by the gene directly by means of two different primary products, (2) they may be produced by the gene by means of the same product, or (3) the gene may produce only one effect A which, in turn, conditions B (indirect gene action). In the latter two, unity of gene action is maintained (spurious pleiotropism), whereas only the first case would constitute genuine pleiotropism. Grüneburg postulated that genuine pleiotropism does not exist. He suggested that cases where a character cannot be fitted into the developmental picture might best be accounted for by our own ignorance.

Dobzhansky in Goldschmidt (1955) pointed out that the difficulty in Grüneburg's classification is that primary effects of genes

are unknown. Hence, it is futile to classify recorded instances into real and spurious ones.

Caspari (1952) believed evidence exists that pleiotropic effects of genes are common. His reasoning is based on the interaction of biochemical processes at the level of gene action both at the developmental and embryological stages.

Throughout the manuscript as in the preceeding review of single gene effects in poultry the gene symbolism used is that suggested by Jaap and Hollander (1954). Genes of the standard wild type are designated by the same letter as the mutant gene with a + superscript.

Jaap and Grimes (1956) reported that the dominant white gene (I) when introduced into the Barred Plymouth Rock breed suppressed growth. Their conclusions based on observations from 19,211 progeny were that, I interacts with the gene for extension of black throughout the plumage (E) to suppress body weight at eight weeks of age. Growth rate was further suppressed when the gene responsible for barred plumage (B) was also present with genes I and E. The average effect of I and E was to suppress body growth by .03 to .04 pounds by eight weeks of age. When B was present suppression was increased to .06 to .07 pounds. Evidence also indicated that the genes for silver (S) and slow feathering (K) also interact with I to suppress body growth, but these genes do not augment growth suppression already present from the interaction of I

with E and B.

Jerome, et al. (1956) introduced dominant white into the Barred Plymouth Rock. Barred chickens showed superiority over the whites in growth and feed efficiency to 10 weeks of age. Collins and Hubbard (1957) also reported that the growth rate of heterozygous dominant white chicks, which carried at least one dominant gene each for E, B, and S, was reduced by .07 pounds. This study also showed that parents heterozygous for I and E produced a smaller percent of white than of colored offspring, and parents heterozygous for I but homozygous for e^+ produced white and colored offspring in approximately equal numbers. These data also suggest that the interaction of I and E may have reduced viability of the embryo.

Mérat (1959d) compared the eight week weight of heterozygous dominant white chicks (Ii^+) with carriers of the recessive wild allele (i^+i^+). The chicks originated from the same mating. A highly significant difference of 30 grams favored the wild type females. Comparable differences were not found in males.

Williams, et al. (1959) reported the effects of the color genes I, E and B on growth rate. Matings were designed such that only two of these genes were segregating in any one mating. The Ee genotype was found to be superior to ee for growth to nine weeks of age. Average differences of 62 and 33 grams for males and females, respectively, were reported. An

increase in body weight was observed when I replaced i^+. When I and B were together an increase in weight was also observed. This result is contradictory to the findings of other workers.

Recessive white (cc) was investigated by Jerome, et al. (1959). Colored chicks (C^+c) were found to have significantly faster growth rate to nine weeks of age than white chicks (cc). In a line established by backcrossing F_1 females from a Brown Leghorn x White Plymouth Rock cross to the white line, Smythe and Fox (1961) also reported growth depression of the recessive white genotype (cc). However the population was known to be segregating at the E, B and S loci in addition to c.

Mérat (1959c) reported a variable effect of the barring gene on growth rate. Members of the same full-sib families of the Gatinaise and Marans breeds were compared. In one population the body weight of non-barred females was significantly greater than that of barred females. Differences were less marked in males, while in crosses involving other breeds the barring gene showed no effect on body weight.

Mérat (1958) investigated another allele of the E series. "Columbian" (ee) type chicks were compared with wild (e^+e^+) type chicks for body weight at four and eight weeks of age. Differences in favor of the wild type (40 grams for males and 30 grams for females) at eight week body weight were noted.

In another study, Mérat (1959b) found that the gene W^+, which controls yellow pigmentation of the shank and skin, also

influenced mortality. The percentage mortality at eight weeks of age for white shanked (W+w) birds was 27.3 and for yellow shanked (ww) birds was 22.3. This difference in survival rate of chicks with yellow shanks approached the one percent level of significance.

The sex-linked gene K, which influences rate of feather growth, has also been studied with respect to its effect on growth and mortality. Godfrey (1952) reported that the recessive gene (k^+) for rapid feathering did not influence growth rate or mortality to ten weeks of age.

Kan, et al. (1959) reported the effect of the gene for pea comb (P) on six metric traits in meat type chickens. This gene in the absence of the rose comb gene (R) determines pea comb. The six traits were: six week body weight, housing body weight, number of eggs set during the first sixteen weeks of production, number of eggs laid during the first six months of production, percent fertile eggs set and percent hatch of fertile eggs. Gene P appeared to have no influence upon the traits studied. However, there was some indication that single comb (p^+p^+) birds tended to be heavier at housing. Further investigations of pea comb by Collins, et al. (1961) revealed that single comb birds (p^+p^+) were generally heavier at nine weeks of age than pea comb birds (Pp^+).

Mérat (1959a) studied the gene R which determines rose comb. A deficiency of rose comb progeny (Rr^+) was noted in

crosses of rose comb males (Rr^+) on single comb females (r^+r^+). However, abnormal proportions for some males and normal proportions for others were found.

METHODS AND MATERIALS

Mating Procedures

The procedure in forming a line heterozygous at a particular locus is described by Fisher (1949). An already established inbred line is outcrossed to bring in a desired gene. The heterozygote is then backcrossed in successive generations, keeping the desired gene in a heterozygous state, but increasing the percentage of blood of the inbred line in each successive backcross. The procedure is illustrated in Figure 1. A more detailed description of the actual matings is found in the section, Heterozygous Inbred Lines and Segregating Populations. The number of birds housed and phenotypes for the 1959 non-segregating backcross generations and the 1960 segregating populations are presented in Table 1.

Genes Introduced

Dominant white

The white plumage color common to White Leghorns is dominant to black. It is not dominant to red plumage, since red progeny result from crosses between dominant white and red breeds.

Dominant white was one of the first characters in poultry shown (by Bateson in 1902) to be inherited in accordance with Mendel's laws. The gene in question was later given the symbol I (inhibitor of black pigment) by Hadley in 1913.

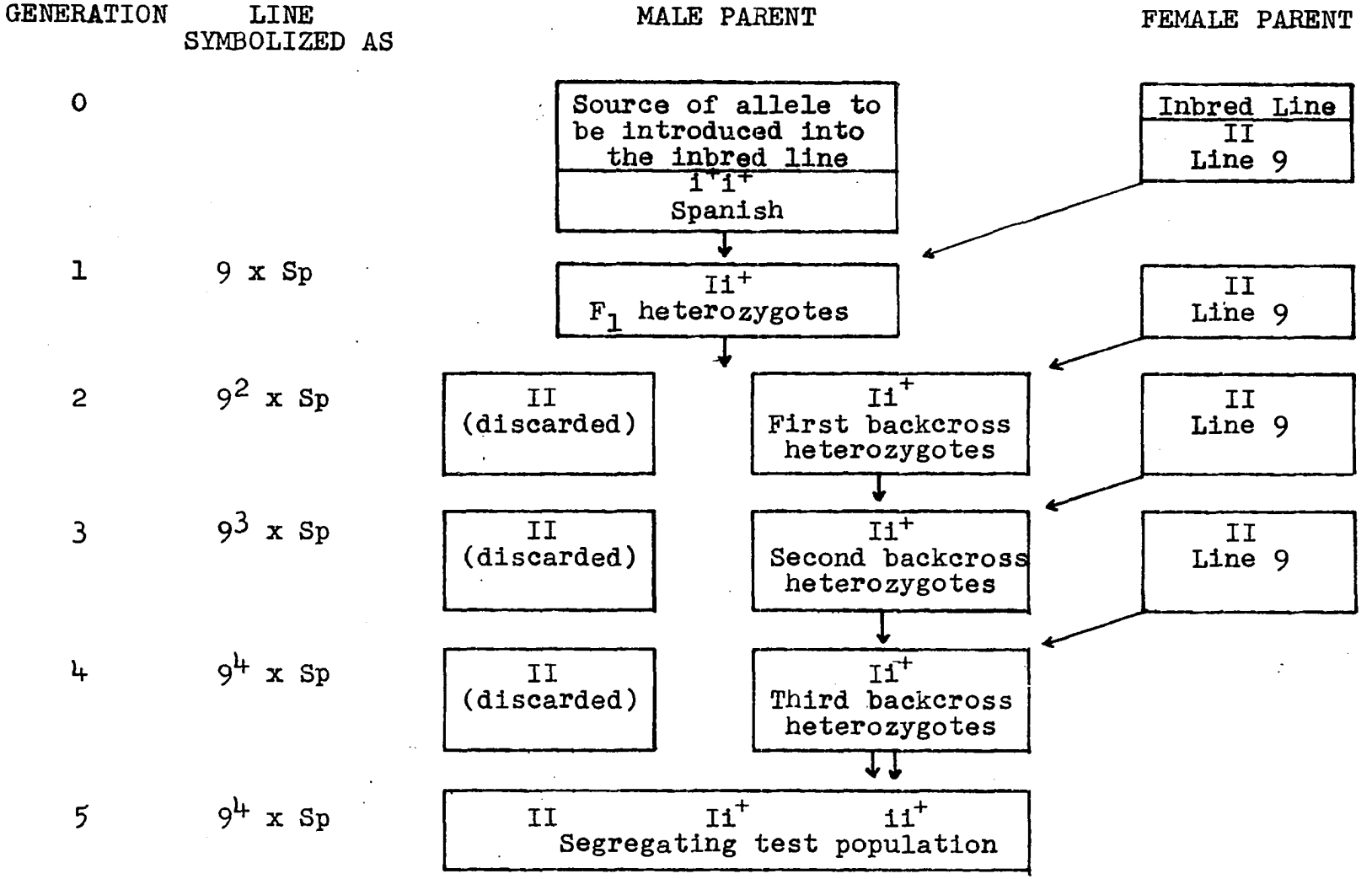

Figure 1. Backcross mating scheme illustrating the introduction of gene i into Leghorn Line 9

Table 1. Summary of 1959[a] heterozygous lines and 1960 segregating populations

Lines heterozygous for:	Year of origin	No. of female breeders	Phenotype and genotype of matings: Male	Female
			1959	
Dominant White (I)				
9^4 x SP	1955	37	White (Ii^+)	White (Ii^+)
Ba^4 x SP	1955	25	White (Ii^+)	White (Ii^+)
Sp^4 x 9	1954	82	Black Fleck (Ii^+)	39 Bl. Fleck (Ii^+) 43 Bl. (i^+i^+)
Sp^4 x BA	1954	63	Black Fleck (Ii^+)	33 Bl. Fleck (Ii^+) 30 Bl. (i^+i^+)
Rose Comb (R)				
9^4 x WL	1955	49	Rose Comb (Rr^+)	Rose Comb (Rr^+)
19^4 x WL	1955	23	Rose Comb (Rr^+)	Rose Comb (Rr^+)
HN^4 x WL	1955	31	Rose Comb (Rr^+)	Rose Comb (Rr^+)

	No. of pullets	Phenotypes produced		
		1960		
Dominant White (I)				
9^4 x SP	222	216 White		6 Barred or blue
Ba^4 x SP	103	81 White		22 Barred or blue
Sp^4 x 9	260	25 White	121 Black Fleck	114 Black
Sp^4 x BA	254	47 White	117 Black Fleck	90 Black
Rose Comb (R)				
9^4 x WL	293	224 Rose Comb		69 Single Comb
19^4 x WL	197	149 Rose Comb		48 Single Comb
HN^4 x WL	163	114 Rose Comb		49 Single Comb
Barring (B)				
Barred SR	107	58 Barred		49 Non-barred

[a]Third backcross individuals represent 93.75 percent of parent inbred line blood.

This gene seems to act upon melanophores in the developing feather follicle. Hamilton (1940) in studying melanophores found differences in the viability of melanophores. Those from dominant white material degenerated at the earlier stages.

Rose comb

This type of comb, determined by a dominant gene (R), is characterized by a low flat head appendage covered with smooth, even papillae and terminating with a spike.

The genetics of rose comb was first reported by Bateson in 1902 and is one of the first examples of Mendelism in animals.

Sex-linked barring

Barring (B) was reported to be sex-linked by Spelman in 1908. This was confirmed by Goodale and others in 1910.

The barring gene restricts the deposition of melanin to bars in the feather that would otherwise be a solid color. The width and sharpness of the barring differs in the two sexes. Barring varies according to strains and birds within strains. Also different regions of the plumage within one bird show variation of barring. Barring apparently enhances the inhibiting action of the dominant white gene.

Heterozygous Inbred Lines and Segregating Populations

Heterozygous inbred lines are those which are heterozygous for a particular morphological trait. These lines are symbolized as follows:

$$A^n \times B$$

where, A is the parent inbred line to which backcrossing has been made n generations after the original outcross to line B to introduce the segregating gene. Segregating lines or populations are established by inter se matings of heterozygous inbred lines.

Parent inbred lines are those used in the backcross matings. These are as follows:

Lines 9 and 19 are inbred Leghorn lines originating, respectively, in 1939 and 1944 at the Iowa Station. In 1956, Line 9 had reached an inbreeding coefficient of 93 percent and Line 19 a coefficient of 68 percent. Since then they have been maintained by flock mating.

Lines BA and HN are relatively new Leghorn lines originating from two different commercial breeders in 1954. Inbreeding in these lines reached 39 and 40 percent, respectively, by 1958.

Line SP represents a Spanish breed (Castillana Negra) obtained as hatching eggs in 1954 from the University of Minnesota. They have since been maintained as a closed flock.

The breed is similar to the Black Minorca in color and body shape.

Dominant white Leghorn lines

Dominant white was made heterozygous in two inbred Leghorn lines, 9 and BA. Since the Leghorn breed normally carries the dominant allele (I), the recessive allele (i^+) was obtained from the Spanish line. The two Leghorn lines segregating for dominant white are symbolized 9^4 x Sp and BA^4 x Sp.

The formation of these two segregating lines was similar. The initial cross from a male of each inbred Leghorn line on Spanish females was made in 1955. Backcrosses were made in 1956, 1957 and 1958. One or two pens of four to six heterozygous females (Ii^+) each were mated to an inbred Leghorn male.

In order to identify the heterozygous individuals it became necessary to progeny test after the second backcross generation; heterozygous and homozygous genotypes were no longer distinguishable by a difference of black flecking in the plumage.

All three genotypes at the dominant white locus (II, Ii^+ and i^+i^+) were produced from the heterozygous inbred lines in 1959. In Line 9^4 x Sp, 37 progeny tested heterozygous females and four progeny tested heterozygous males were mated. Also, 25 progeny tested heterozygous females in Line BA^4 x Sp were

mated to three progeny tested heterozygous males.

Dominant white Spanish lines

Two heterozygous dominant white lines were formed. The dominant allele was obtained from Leghorn Lines 9 and BA. These segregating lines were symbolized Sp^4 x 9 and Sp^4 x BA.

The initial cross of males from each of the Leghorn lines on Spanish females was made in 1954. The mating of heterozygous backcross female progeny to Spanish males was practiced in 1955 and 1956. In 1956 inter se matings of two pens of heterozygous individuals resulted in all three genotypes of (I, i^+). Performance records were not taken in this generation. In 1958 a further backcross was made using three pens of each line, and using both the heterozygous (Ii^+) and homozygous recessive (i^+i^+) females. In 1959, segregating generations were obtained from a mating of eight heterozygous males of each line and 63 heterozygous and homozygous females for Line Sp^4 x BA and 82 females of Line Sp^4 x 9. Progeny representing all three genotypes of I were then performance tested.

Rose comb lines

The dominant rose comb allele (R) was introduced into three single-comb inbred Leghorn lines; 9, 19 and HN in 1955. The source of the allele was a White Wyandotte x Leghorn male, symbolized WL. In 1960 all three genotypes of rose comb were

performance tested. Three breeding pens per line were used to produce the backcross generations. In the 1959 matings, the number of heterozygous female breeders for Lines 9^4 x WL and HN^4 x WL were 87, 23 and 31, respectively.

Barred Spanish

The barred Spanish line originated from a single barred male which appeared in the Sp line in 1956. Testing proved it to be sex-linked. Inbreeding was practiced with planned heterozygosis at the barring locus. In 1959 a flock mating of 28 females and two males produced the progeny representing the 1960 test flock. The inbreeding among individuals in the flock mating ranged from 27.3 to 42.0 percent.

Traits Studied

Changes in phenotypic expression for dominant white and rose comb were noted in each backcross generation.

The 1960 segregating populations were obtained in three to five hatches as follows:

Hatch dates	Lines
February 9	All Lines
February 22	All Lines
March 8	All Lines but Spanish Lines
March 22	(9^4 x Sp), (BA^4 x Sp), (19^4 x WL), (HN^4 x WL), Barred Sp.
April 6	(9^4 x Sp), (BA^4 x Sp), (19^4 x WL), (HN^4 x WL)

Birds were brooded at the Ames Poultry Farm until eight weeks of age at which time they were vaccinated for fowl pox

and placed on summer range at the Ankeny Experimental Farm. All birds were removed from range on August 17, 18 and 19, 1960, and placed in pens according to segregating lines.

Standard feeding and management practices were followed during the brooding, range and laying periods for all lines.

Data were obtained on the following traits of the segregating populations:

	Measured in
Body weight at eight weeks	decigrams
Body weight at housing	pounds
Body weight in December	pounds
Egg weight (December)	grams
Egg number in Period 1	Number of eggs
Egg number in Period 2	Number of eggs

Egg production periods were:

Period 1: September 6 - December 28
Period 2: February 14 - April 19

Only birds which were present at the three measurement periods were used in the body weight analyses.

Average egg weights, based on the last four trap nest days of Period 1, were obtained for each individual test pullet.

Birds were trapnested two days per week and only records of individuals producing at least one egg were used. This eliminated records of birds laying on the floor. Only birds surviving the period were used. Data on sexual maturity were not considered sufficiently reliable to use because many birds were laying at the time of housing.

Progeny Testing

Dominant white segregating lines

After the second backcross of dominant white heterozygotes to the inbred Leghorn parent lines, the heterozygotes no longer exhibited black flecking in their plumage and consequently they were phenotypically indistinguishable from the homozygous dominant whites.

It was therefore necessary to progeny test to identify the homozygous and heterozygous genotype by mating to a recessive tester. Males from the Spanish line (Sp) served as testers. One homozygous recessive (i^+i^+) offspring from a test mating permitted the classification of the individual as a heterozygote. Such an individual was then eligible to be used in the next backcross mating. In the segregating lines, since dominant white was present in all three genotypes, it was necessary to progeny test in order to classify genotypes.

All females of the segregating populations were test mated to homozygous (i^+i^+) males. Depending on the test progeny produced these females were classified as follows:

Test progeny	Genotype of test birds
Seven or more white	Homozygous dominant (II)
White and black	Heterozygous (Ii^+)
Seven or more black	Homozygous recessive (i^+i^+)

To classify an individual as a homozygote, seven or more of one type of progeny were arbitrarily required. The maximum probability then of misclassifying a heterozygous individual

as a homozygote would be $(1/2)^7$ or .0078.

Rose comb lines

No progeny testing was required during the backcross generations since rose comb is dominant. In the segregating populations progeny testing was required to distinguish homozygous and heterozygous rose comb genotypes. Homozygous recessive or single comb individuals were phenotypically distinguishable.

All rose comb females were progeny tested to single comb males. Females were then classified as follows:

Test progeny	Genotype of test bird
Seven or more rose comb	Homozygous (RR)
One single comb	Heterozygous (Rr^+)

Adjustment of Data

Progeny testing was conducted during the first egg production period. In both rose comb and Leghorn dominant white lines a minimum of seven test progeny was arbitrarily set to designate the homozygous genotypes. However, this introduced a bias into the results because it favored the classification of the better producers. Examination of egg production records of individuals which were classified as homozygotes showed that the lower production levels were not represented. To estimate the probable number of individuals in the lower production levels, all individuals producing at least one test progeny were used. The data were then treated

in the following manner.

Rose comb lines

Let lower case letters (a) be the observed number and upper case letters (A) represent the estimated number of individuals in a class. Let the subscript k be the total number of eggs laid in period 1 and k' the number of eggs sampled and hatched for progeny testing.

For the heterozygous group the observed number of individuals in a class (y) were those birds which produced at least one homozygous or single comb progeny. The estimated number of heterozygotes (Y) is the difference of the total heterozygotes in that class and those classified as homozygotes. The probability of producing a homozygous recessive offspring when testing against a homozygous recessive tester was used to estimate individuals incorrectly classified. The equation is,

$$y_{kk'} = Y_{kk'} - 1/2^{k'} Y_{kk'}$$
$$= (1 - 1/2^{k'}) Y_{kk'}$$

For the homozygous group the observed number of individuals in a class (x) were those birds which produced no homozygous recessive test progeny. The estimated number of homozygotes (X) is the sum of all homozygotes in that class plus those heterozygotes incorrectly classified. This is represented as follows:

$$x_{kk'} = X_{kk'} + 1/2^{k'} \; Y_{kk'}$$

Solving for the estimated number of individuals in a class which laid a particular number of eggs:

$$Y_{k.} = \sum_{k'} Y_{kk'}$$

$$= \sum_{k'} \frac{ykk'}{1 - 1/2^{k'}}$$

and

$$X_{k.} = \sum_{k'} X_{kk'}$$

$$X_{k.} = \sum_{k'} (x_{kk'} - 1/2^{k'} \; \frac{ykk'}{(1-1/2^{k'})})$$

$$X_{k.} = \sum_{k'} (x_{kk'} - \frac{ykk'}{2^{k'} - 1})$$

No progeny testing was performed on the homozygous recessives or single comb group. These were symbolized as follows:

$$z_{kk'} = Z_{kk'}$$

The estimated egg production obtained as above for each individual was then used in a subsequent least squares analysis.

Leghorn dominant white lines

Progeny testing was used in Lines 9^4 x Sp and BA^4 x Sp in order to identify the three genotypes of dominant white. In Line BA^4 x Sp, progeny testing indicated that the blue or barred phenotype represented the homozygous recessive genotype

(i^+i^+). However, three individuals classified as recessives by progeny test exhibited an all white phenotype. Therefore, the following treatment was applied to the first period egg production data of both lines.

The symbolism corresponds to that used in the previous section. Lower case letters represent the observed number and upper case letters the estimated number of individuals in a class. The subscripts k and k' again represent the total number of eggs laid and the number of eggs sampled for progeny test, respectively.

Individuals which produced both black and white test progeny were classified as heterozygotes and represent the observed number (y) in that class. When all three genotypes are tested, misclassification can occur for both homozygous classes. Accordingly, the estimated number (Y) would lose individuals to both homozygous classes. The estimation then is as follows:

$$y_{kk'} = (1 - 1/2^{k'} - 1/2^{k'})\, Y_{kk'}$$

then

$$Y_{k.} = \sum_{k'} \frac{y_{kk'}}{1 - 2(1/2^{k'})}$$

Individuals which produced only white individuals represent the observed homozygous dominants (x). The corresponding expected number (X) would also include the misclassified heterozygotes.

$$x_{kk'} = X_{kk'} + 1/2_{k'}\ Y_{kk'}$$

then

$$X_{k.} = \sum_{k'} x_{kk'} - 1/2^{k'}\ \left(\frac{ykk'}{1-2\ (1/2^{k'})}\right)$$

$$X_{k.} = \sum_{k'} x_{kk'} - \frac{ykk'}{2k' - 2}$$

The same follows for individuals which produced only black individuals and represent the homozygous recessives group.

$$Z_{k.} = \sum_{k'} z_{kk'} - 1/2^{k'}\ \frac{y_{kk'}}{1-2\ (1/2^{k'})}$$

$$Z_{k.} = \sum_{k'} z_{kk'} - \frac{y_{kk'}}{2k' - 2}$$

A least-squares analysis was then conducted on egg number (k) for the estimated population.

Statistical Methods

General model

Estimates of the parameters were obtained by application of the method of least-squares using the model:

$$Y_{ijkl} = u + l_i + g_{ij} + h_k + e_{ijkl}$$

where: Y_{ijkl} = observed value of the l^{th} chicken of the k^{th} hatch of the j^{th} genotype within the i^{th} line

u = general population mean

l_i = effect of the i^{th} line

g_{ij} = effect of the j^{th} genotype within the i^{th} line

h_k = effect of the k^{th} hatch

e_{ijkl} = deviation of the l^{th} chicken from the mean of the ij^{th} genotype and of the k^{th} hatch.

The assumption was made that the hatch x genotype within lines and hatch x line interactions were negligible.

The generalized normal equations are presented in a tabular form, as follows:

	$\hat{u}$	$\hat{l}_i$	$\hat{g}_{ij}$	$\hat{k}$	RHS
u	$n_{...}$	$n_{i..}$	$n_{ij.}$	$n_{..k}$	$Y_{...}$
l_i		$n_{i.}^{o}$	$n_{ij.}$	$n_{i.k}$	$Y_{i..}$
g_{ij}			$n_{oij.}^{o}$	n_{ijk}^{o}	$Y_{ij.}$
h_k				$n_{..k}^{oo}$	$Y_{..k}$

The elements to the left of the main diagonal in this coefficient matrix are omitted since they would be the same as those to the right of the main diagonal. The n_o^o symbol in the various sections of the matrix indicates that the off-diagonal elements of these submatrices are equal to zero. The replacement of a subscript by a dot denotes summing over that subscript. The RHS denotes the right hand sides of the normal

equations and is the sum of the observations in that class ($Y_.$).

To obtain an unique solution to the equations the restrictions chosen were:

$$\sum_{1} l_i = \sum_{j} g_{ij} = \sum_{k} h_k = 0$$

Under these restrictions a reduced coefficient matrix and reduced right hand members of the normal equations (RHS) are formed.

Computing estimates

Although the parameter estimates may be obtained by direct solution of the equations, the estimates were computed from the inverse elements of the reduced coefficient matrix multiplied by the reduced right hand sides (RHS) of the normal equations.

Since:

$$\sum_{j} C^{ij} Y_j = \hat{C}_i$$

where C^{ij} is the inverse element for the i^{th} row and the j^{th} column of the complete inverse matrix, Y_j is the RHS for the j^{th} row and C_i is the i^{th} parameter estimate.

Computing sums of squares

The reduction in sums of squares due to fitting all parameters was computed from the parameter estimates multiplied

by the reduced RHS. The error sums of squares is equal to

$$\sum_{ijkl} Y^2_{ijkl} - R(\hat{u}, \hat{l}_i, \hat{g}_{ij}, \hat{h}_k)$$

where: $\sum_{ijkl} Y^2_{ijkl}$ is total sums of squares and $R(\hat{u}, \hat{l}_i, \hat{g}_{ij}, \hat{h}_k)$ is the reduction due to fitting all parameters.

The sums of squares for the other classes were obtained as follows:

$$S.Sgs. = B'Z^{-1} B$$

where: B' is a row vector of the parameter estimates for a given set (such as l_i); Z^{-1} is the inverse of the segment of the inverse of the reduced coefficient matrix corresponding, by row and column, to this set of parameter estimates; and B is a column vector of the set of parameter estimates. The sum of squares is then equal to the reduction in the sum of squares due to fitting all parameters minus the reduction in sum of squares due to fitting all parameters except the set being considered.

The analysis of variance is presented as follows:

Source	d.f.	EMS
Hatches	h - 1	$\sigma e^2 + k_3 \sigma_h^2$
Lines	L - 1	$\sigma e^2 + k_2 \sigma_l^2$
Genotypes within Lines	s - 1	$\sigma e^2 + k_1 \sigma^2_{g/l}$
Error	N-h-s+2	σe^2

where: h is number of hatches

L is number of lines

s is number of genotype within line subclasses

N = n...

The Lines and Genotypes within Lines were considered fixed effects and Hatch was considered a random effect.

Individual comparisons

If the Genotypes within Lines mean square was statistically significant, the corresponding parameter estimates were subjected to the "t" test.

The ratio distributed as "t" is defined as

$$t = \frac{\hat{g}_i - \hat{g}_j}{\sqrt{(C_{g_ig_i} + C_{g_jg_j} - 2C_{g_ig_j})\,\sigma e^2}}$$

where: $g_i - g_j$ represents the estimated genotype difference within a line, the C's identify the elements of the matrix inverse of the reduced coefficient matrix and σe^2 is the mean square for error.

Reduced model

Sex-linked barring was segregating in one line, and no line effect could be estimated. The model is as follows:

$$y_{ijk} = (u + l) + g_i + h_j + e_{ijk}$$

where: y = observed value of the k^{th} chicken of the j^{th}

hatch of the i^{th} genotype

$(u+l)$ = general population mean plus the line effect

g_i = effect of the i^{th} genotype

h_j = effect of the j^{th} hatch

e_{ijk} = deviation of the k^{th} chicken from the mean of the i^{th} genotype and the j^{th} hatch.

The analysis of variance is as follows:

Source of variation	d.f.	EMS
Hatch	h - 1	$\sigma^2e + K_2 \sigma^2h$
Genotype	g - 1	$\sigma^2e + K_1 \sigma_g^2$
Error	N - h - g + 2	σ^2e

In this case genotype x hatch interaction was assumed to be negligible.

RESULTS

The Expression of Dominance

Dominant white (I)

The heterozygotes originating from the Leghorn parental inbreds differed from those originating from the Spanish parental inbred lines in that the plumage of the latter became darker with each successive backcross generation. This is illustrated in Figure 2. The mating of third generation backcross heterozygotes produced all three genotypes (Figures 3, 4 and 5). The homozygous dominant (II) is pure white. The heterozygote (Ii^+) is black-flecked and the homozygous recessive (i^+i^+) is black. The gene I then in a Spanish background is incompletely dominant.

Since no difference was observed between dominant white alleles from sources, Lines 9 and BA, with respect to dominance, it seems that the differences observed are due to the genetic background and not to the source of the I genes.

Heterozygotes of the first backcross to the Leghorn Lines, 9 and BA, were distinguishable by slight black flecking in the plumage. However, heterozygotes of the second and third backcross had no flecking so that progeny testing was necessary to identify heterozygous individuals.

Segregating matings ($Ii^+ \times Ii^+$) in Line 9 produced all three genotypes of dominant white. The ratio obtained was

216 white to 6 barred or blue individuals. Progeny testing of the white plumaged individuals reaching sexual maturity to recessive i^+i^+ males proved that 36 were in fact recessive genotypes (i^+i^+), but that the gene for recessive white (c) was present. The gene frequency of c within the recessive (i^+i^+) class yielded an estimate of $q_c = \sqrt{\frac{36}{42}} = .93$.

However, even with the high frequency of the c gene, no black-flecked birds were noted; I in this Leghorn background was a complete dominant.

In Line BA, the segregating mating, ($Ii^+ \times Ii^+$) produced a ratio of 81 white and 22 blue or barred individuals which agreed well with the expected three to one ratio. The blue or barred individuals, when progeny tested, proved to be of the recessive genotype (i^+i^+). However, three all white individuals again proved to be recessive (i^+i^+) with 8, 9 and 16 all black or blue test progeny, respectively. Thus, recessive white was also present in Line BA, at an approximate gene frequency of .35. Since no black flecked individuals were observed, I was also completely dominant in the BA Leghorn Line. Figure 6 pictures an all white progeny tested heterozygote (Ii^+) of the Leghorn backcross, ($9^4 \times Sp$) and a black-flecked heterozygote of the Spanish backcross, ($Sp^4 \times 9$).

Rose comb (R)

Rose comb heterozygotes were backcrossed only to the single comb Leghorn parent. In the second backcross a

modified spike of the rose comb simulating a single comb blade was noted. Figure 7 presents a typical example of a second generation backcross. This individual shows a prominent blade at the rear of the comb. A more extreme example is presented in Figure 8. Here, even the normal papillae of the rose comb are greatly reduced.

Production of all three genotypes from heterozygous matings ($Rr^+ \times Rr^+$) yielded the expected ratio of three rose comb to one single comb in each of the three lines. Progeny testing was necessary to distinguish between heterozygous (Rr^+) and homozygous (RR) individuals. Thus, rose comb was completely dominant in all three single comb lines, but its form became modified in successive backcross generations.

With the formation of the segregating populations several cross-beaked birds were noted in the rose comb individuals of two lines. Line 9^4 x WL exhibited no cross-beaks. In Line 19^4 x WL four cross-beaks were observed. Two of these were classified by progeny testing as homozygous dominant rose comb (RR). Line HN^4 x WL produced six cross-beaks of which three were the homozygous (RR) and one the heterozygous (Rr^+) genotype.

Effect of Segregating Genotype on Metric Traits

The following symbolism is used:

$\hat{u}$ = general population mean

$\hat{l}_i$ = effect of the i^{th} line

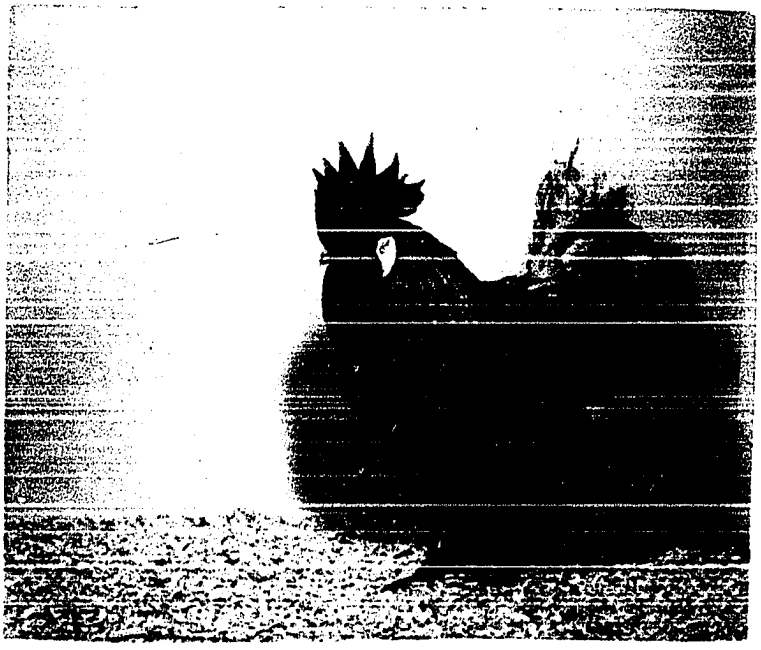

Figure 2. A heterozygote of the second Spanish backcross

Figure 3. A homozygous dominant (II) of the Spanish segregating lines

Figure 4. A heterozygote (Ii^+) of the Spanish segregating lines

Figure 5. A homozygous recessive (i^+i^+) of the Spanish segregating lines

Figure 6. An all white progeny tested heterozygote (Ii^+) of the Leghorn segregating lines and a black-flecked heterozygote (Ii^+) of the Spanish segregating lines

Figure 7. A typical second backcross heterozygote of rose comb

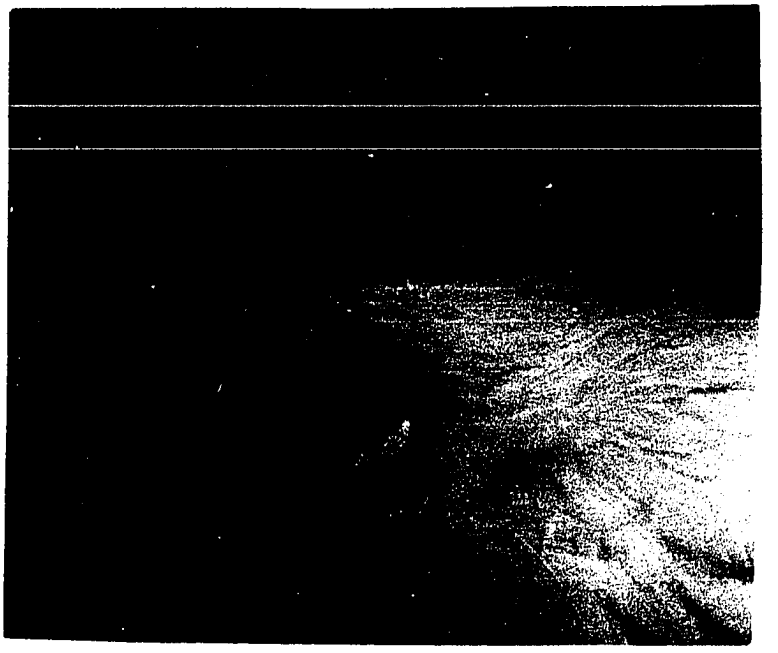

Figure 8. An extreme second backcross heterozygote of rose comb

$\hat{g}_{ij}$ = genotype effect in the i^{th} line of a particular locus under study where subscript (j) denotes the genotype as follows:

2, two dominant alleles (AA)

1, one dominant allele (Aa)

0, no dominant allele (aa)

$\hat{h}_k$ = effect of the k^{th} hatch, k = 1, 2 --- 5.

The normal equations, the reduced equations (formed by imposing the restrictions) and the matrix inverse of the reduced coefficient matrix for the follow least-squares analyses are presented in the Appendix. Since all matrix tables are symmetrical, the elements to the left of the main diagonal are omitted.

Dominant white in Spanish lines

Two segregating populations were formed in the Spanish background: Lines Sp^4 x 9 and Sp^4 x BA. These lines are symbolized in the tables by the subscripts 9 or BA.

Body weight Parameter estimates of $\hat{u}$, $\hat{l}$, $\hat{g}$ and $\hat{h}$ for each of the three weigh periods are presented in Table 2.

The mean squares for the various sources of variation in all three weigh periods are given in Table 3.

Individual genotype within line estimate comparisons by the use of "t" tests are presented in Table 4.

The effect of I on body weight revealed that in the Spanish lines, the recessive genotype was superior at all

Table 2. Parameter estimates for body weights at three ages in the Spanish lines segregating for dominant white (see corresponding Appendix Tables 28, 29 and 30)

	Estimate :	Age		
		8 weeks (decidgrams)	Housing (pounds)	December (pounds)
Pop. mean	$\hat{u}$	66.3852	3.6046	3.9949
Line effects	$\hat{l}_{BA}$	-1.4800	-.0310	-.0549
	$\hat{l}_{9}$	+1.4800	+.0310	+.0549
Genotype effects (Line BA)	$\hat{g}_{BA,2}$	-1.2121	-.0382	-.1253
	$\hat{g}_{BA,1}$	- .3746	-.0212	-.0072
	$\hat{g}_{BA,0}$	+1.5867	+.0594	+.1325
(Line 9)	$\hat{g}_{9,2}$	+1.0910	-.1258	-.2356
	$\hat{g}_{9,1}$	-2.2506	-.0157	+.0666
	$\hat{g}_{9,0}$	+1.1596	+.1415	+.1690
Hatch effects	$\hat{h}_{1}$	+1.8293	+.0502	-.0209
	$\hat{h}_{2}$	-1.8293	-.0502	+.0209

Table 3. Analyses of variance of body weight at three ages in the Spanish lines segregating for dominant white

Source	d.f.	Mean squares		
		8 week	Housing	December
Hatches	1	1425.07[a]	1.064[b]	.186
Lines	1	792.88[a]	.004	1.091
Genotype/Lines	4	259.58[b]	.665[b]	1.384[a]
Error	502	40.64	.252	.365

[a]Significant at .01 level.

[b]Significant at .05 level.

Table 4. Intra-line body weight deviations for dominant white genotypes in the Spanish background

Genotype:Line	Ii^+	i^+i^+
	Eight week weight (decigrams)	
II:BA	+ .8375	+2.7988[a]
:9	-3.3416[a]	+ .0686
Ii^+:BA		+1.2121[a]
:9		+3.4102[b]
	Housing weight (pounds)	
II:BA	+ .0170	+ .0976
:9	+ .1101	+ .02673[a]
Ii^+:BA		+ .0806
:9		+ .1572[a]
	December weight (pounds)	
II:BA	+ .1181	+ .2578[a]
:9	+ .3022[a]	+ .4046[b]
Ii^+:BA		+ .1397
:9		+ .1024

[a]Significant at .05 level.

[b]Significant at .01 level.

three ages of measurement. Statistically significant differences were found in three of the four possible comparisons of the recessive genotype (i^+i^+) with either of the dominant white genotypes of Ii^+ and II in both Spanish lines at eight weeks of age. Significance was also noted in two of the four comparisons at the housing and December weigh

periods. Significant differences were also noted in Line Sp^4 x 9 between the two dominant white genotypes II and Ii^+. The heterozygous genotype (Ii^+) was significantly lighter in body weight than the homozygous genotype (II) at eight weeks, but significantly heavier at the December weigh period.

Hatch effects were significant at eight weeks and housing but not for the mature body weight measure in December. A hatch effect would be expected at housing since all hatches were housed on three consecutive days.

A line difference was noted only at the eight weeks weigh period.

The body weight estimates for $\hat{u}$, $\hat{l}$ and $\hat{g}$ are presented in Table 5.

Table 5. Genotype means for body weights in the Spanish lines segregating for dominant white

	Genotype		
	II	Ii^+	i^+i^+
Eight weeks (decigrams)			
Sp^4 x 9	68.9562	67.4906	69.0248
Sp^4 x BA	63.6631	64.5306	66.4919
Housing (pounds)			
Sp^4 x 9	3.5098	3.6199	3.7771
Sp^4 x BA	3.5354	3.5524	3.6330
December (pounds)			
Sp^4 x 9	3.8142	4.1164	4.2188
Sp^4 x BA	3.8147	3.9328	4.0725

Egg production and egg weight The parameter estimates for egg production and egg weight are presented in Table 6.

Table 6. Parameter estimates for egg production and egg weight in the Spanish lines segregating for dominant white (see corresponding Appendix Tables 31-39)

Estimate		Period 1 (no. of eggs)	Period 2 (no. of eggs)	Egg weight (grams)
Pop. mean	$\hat{u}$	13.4318	6.1787	59.2713
Line effect	$\hat{l}_{BA}$	+1.011	+1.4111	+ .5831
	$\hat{l}_{g}$	-1.011	-1.4111	- .5831
Genotype effect (Line BA)	$\hat{g}_{BA,2}$	- .7865	- .3829	- .2898
	$\hat{g}_{BA,1}$	- .4224	- .3026	+ .0313
	$\hat{g}_{BA,0}$	+1.2089	+ .6855	+ .2585
(Line 9)	$\hat{g}_{9,2}$	-1.2568	- .1087	- .1114
	$\hat{g}_{9,1}$	+ .0310	- .0711	- .1972
	$\hat{g}_{9,0}$	+1.2258	+ .1798	+ .3086
Hatch effects	$\hat{h}_{1}$	- .4589	+ .0619	- .1490
	$\hat{h}_{2}$	+ .4589	- .0619	+ .1490

The mean squares obtained from the analysis of variance for both periods of egg production are given in Table 7.

Significant line differences were noted in both periods of measurement, but no genotype or hatch effects were obtained.

The analysis of variance of egg weight is given in Table 8.

Table 7. Analyses of variance of egg production periods in the Spanish lines segregating for dominant white

Source	Period 1		Period 2	
	d.f.	M.S.	d.f.	M.S.
Hatches	1	7.491	1	1.288
Lines	1	291.860[a]	1	481.340[a]
Genotypes/lines	4	70.955	4	13.105
Error	430	40.369	407	17.670

[a]Significant at .01 level.

Table 8. Analysis of variance of egg weight in the Spanish lines segregating for dominant white

Source	d.f.	Mean squares
Hatches	1	4.859
Lines	1	53.562
Genotypes/lines	4	3.025
Error	253	15.289

The means ($\hat{u} + \hat{l} + \hat{g}$) of the three segregating genotypes are presented in Table 9.

No effect of I could be demonstrated on egg production and egg weight.

No line or hatch effects were noted in the egg weight analysis; however, the line mean square did approach the .05 level of significance.

Egg weight means for the segregating genotypes of

Table 9. Egg production and egg weight means in the Spanish lines segregating for dominant white

Lines	Genotype II	Ii$^+$	i$^+$i$^+$
Period 1 egg production (No. of eggs)			
Sp^4 x 9	11.1639	12.4517	13.6465
Sp^4 x BA	13.6564	14.0205	15.6518
Period 2 egg production (No. of eggs)			
Sp^4 x 9	4.6589	4.6965	4.9474
Sp^4 x BA	7.2069	7.2872	8.2753
Egg weight (grams)			
Sp^4 x 9	58.5768	58.4910	58.9968
Sp^4 x BA	60.1442	59.8231	60.1129

dominant white within the two Spanish lines are presented in Table 9.

Dominant white in Leghorn lines

Dominant white (I) segregating populations were formed in two lines of inbred Leghorn background; 9^4 x Sp and BA^4 x Sp. The source of the recessive allele for both lines was the Spanish. These segregating lines are denoted in tables by the subscripts 9 and BA.

Body weight Only birds which were classified by genotype by progeny testing were used in the analyses.

The parameter estimates obtained by multiplying the

reduced coefficient inverse by the reduced right hand sides of the equations for each body weight period are presented in Table 10.

The analysis of variance of the three body weight periods are given in Table 11.

Hatch differences were statistically significant at the eight week and housing weigh periods but not in December. Line differences were obtained at housing and the December weigh periods.

Table 10. Parameter estimates of body weights in Leghorn lines segregating for dominant white (see corresponding Appendix Tables 40, 41 and 42)

Estimate		8 weeks (decigrams)	Housing (pounds)	December (pounds)
Pop. mean	$\hat{u}$	58.4690	3.0657	3.7517
Line effects	$\hat{l}_9$	- .2885	-.3303	-.1822
	$\hat{l}_{BA}$	+ .2885	+.3303	+.1822
Genotype effects (Line 9)	$\hat{g}_{9,2}$	-1.2104	-.0505	+.0383
	$\hat{g}_{9,1}$	+ .7719	+.0180	-.0212
	$\hat{g}_{9,0}$	+ .4385	+.0325	-.0171
(Line BA)	$\hat{g}_{BA,2}$	-1.5712	-.1028	-.0995
	$\hat{g}_{BA,1}$	- .2378	+.0107	+.0351
	$\hat{g}_{BA,0}$	+1.8090	+.0921	+.0644
Hatch effects	$\hat{h}_1$	.8422	+.3151	+.0801
	$\hat{h}_2$	+2.2020	+.0189	-.0415
	$\hat{h}_3$	+ .4848	+.0314	+.0812
	$\hat{h}_4$	+ .3067	-.0373	-.0763
	$\hat{h}_5$	-3.8357	-.3274	+.0435

Table 11. Analyses of variance for body weight at three ages in the Leghorn lines segregating for dominant white

Source	d.f.	Mean squares		
		8 week	Housing	December
Hatches	4	165.344[a]	2.264[a]	.2734
Lines	1	12.362	16.203[a]	4.930[a]
Genotypes/lines	4	52.794	.129	.0942
Error	232	36.984	.085	.1393

[a]Significant at .01 level.

Body weight means of the three segregating genotypes of dominant white within each line are presented in Table 12.

Table 12. Body weight means of the Leghorn lines segregating for dominant white

Lines	Genotypes		
	II	Ii^+	i^+i^+
Eight week weight (decigrams)			
9^4 x Sp	56.9701	58.9524	57.7420
BA^4 x Sp	57.1863	58.5197	60.5665
Housing body weight (pounds)			
9^4 x Sp	2.6859	2.7534	2.7679
BA^4 x Sp	3.2932	3.4067	3.4881
December body weight (pounds)			
9^4 x Sp	3.6078	3.5483	3.5524
BA^4 x Sp	3.8344	3.9690	3.8695

In the Leghorn lines, no growth suppression could be demonstrated and no trends were noted, for no one genotype was superior with respect to body weight.

Egg production and egg weight All birds which had one test progeny were used in the analysis of period 1 egg production. The data were then corrected for genotype classification.

Only birds classified by progeny testing according to genotype were used in the period 2 egg production analysis.

The parameter estimates for body egg production periods and egg weight are presented in Table 13.

The mean squares for both production periods are given in Table 14.

A significant line difference was noted for both production periods, but significant hatch differences appeared only in production period 1.

Egg production and egg weight means for the segregating genotypes of each line are presented in Table 16. The difference between genotypes (II) and (Ii^+) within Line 9^4 x Sp in period 2 was significant.

Parameter estimates obtained from the least squares analysis of egg weight in the Leghorn lines segregating for dominant white are presented in Table 15. The mean squares are given in Table 16.

As in period 1 egg production, significant hatch and

Table 13. Parameter estimates for egg production and egg weight in Leghorn lines segregating for dominant white (see corresponding Appendix Tables 43-51)

Estimates		Period 1 (No. of eggs)	Period 2 (No. of eggs)	Egg weight (grams)
Pop. mean	$\hat{u}$	15.9638	9.2970	50.5670
Line effects	$\hat{l}_g$	-2.5628	-1.9691	-2.2803
	$\hat{l}_{BA}$	+2.5628	+1.9691	+2.2803
Genotype effects (Line 9)	$\hat{g}_{9,2}$	- .6362	+ .9471	+ .2009
	$\hat{g}_{9,1}$	+ .8133	-1.4170	+ .0356
	$\hat{g}_{9,0}$	- .1771	+ .4699	- .2365
(Line BA)	$\hat{g}_{BA,2}$	+1.7269	+1.7282	+ .7464
	$\hat{g}_{BA,1}$	-2.0180	- .1782	- .5826
	$\hat{g}_{BA,0}$	+ .2911	-1.5500	- .1638
Hatch effects	$\hat{h}_1$	+1.6959	+ .0831	+1.4573
	$\hat{h}_2$	+ .5864	- .2509	+1.0327
	$\hat{h}_3$	+ .6416	- .1758	+ .9657
	$\hat{h}_4$	- .0771	+ .0718	-1.3721
	$\hat{h}_5$	-2.8468	+ .2718	-2.0836

Table 14. Analyses of variance for egg production periods in the Leghorn lines segregating for dominant white

Source	Period 1 d.f.	Period 1 M.S.	Period 2 d.f.	Period 2 M.S.
Hatches	4	116.084[a]	4	1.399
Lines	1	1,088.290[b]	1	437.858[b]
Genotypes/lines	4	62.598	4	59.962
Error	251	26.463	190	17.897

[a]Significant at .05 level.

[b]Significant at .01 level.

Table 15. Egg production and egg weight means for the Leghorn lines segregating for dominant white

Lines	Genotypes II	Ii+	i+i+
Period 1 (number of eggs)			
9^4 x Sp	12.7650	14.2145	13.2241
BA^4 x Sp	20.2533	16.5084	18.8175
Period 2 (number of eggs)			
9^4 x Sp	8.2650	5.9109	7.7978
BA^4 x Sp	12.9943	11.0879	12.8161
Egg weight (grams)			
9^4 x Sp	48.4876	48.3223	48.0502
BA^4 x Sp	53.5937	52.2647	52.6835

Table 16. Analysis of variance for egg weight in the Leghorn lines segregating for dominant white

Source	d.f.	Mean squares
Hatches	4	81.785[a]
Lines	1	643.560[a]
Genotypes/lines	4	5.093
Error	180	10.934

[a]Significant at .01 level.

lines differences were also obtained in the egg weight analysis, but no effect of I could be demonstrated on egg production and egg weight.

Rose comb lines

Rose comb segregating populations were formed in three lines of inbred Leghorn background: 9^4 x WL, 19^4 x WL and HN^4 x WL.

These segregating lines are denoted in tables by the subscripts 9, 19 and HN, respectively.

Body weight All single comb individuals and those rose comb individuals which were classified by progeny test were used in the analyses.

The parameter estimates obtained for all three weigh periods are presented in Table 17.

The mean squares obtained from the analyses of variance of the three body weight periods are given in Table 18.

No significant genotype within line differences were noted in any of the three weigh periods, but significant hatch and line differences were obtained.

The body weight means for the lines segregating for rose comb are presented in Table 19.

Egg production All birds which had one test progeny were used in the period 1 egg production analysis. The data for period 1 were then corrected for genotype classification. Only birds classified by progeny testing according to genotype were used in the period 2 analysis.

The least-squares estimates for both production periods and egg weight are given in Table 20.

Table 17. Parameter estimates of body weight in Leghorn lines segregating for rose comb (see corresponding Appendix Tables 52, 53 and 54)

Estimate		8 week (decigrams)	Housing (pounds)	December (pounds)
Pop. mean	$\hat{u}$	59.6380	3.0752	3.6458
Line effect	$\hat{l}_9$	-1.3449	-.2090	+.0180
	$\hat{l}_{19}$	- .1505	-.0766	-.2161
	$\hat{l}_{HN}$	+1.4954	+.2856	+.1981
Genotype effect (Line 9)	$\hat{g}_{9,2}$	- .2962	-.0906	+.0256
	$\hat{g}_{9,1}$	+ .3457	+.0192	+.0680
	$\hat{g}_{9,0}$	- .0495	+.0714	-.0936
(Line 19)	$\hat{g}_{19,2}$	- .3151	-.0410	+.0556
	$\hat{g}_{19,1}$	+ .6381	-.0442	-.0051
	$\hat{g}_{19,0}$	- .3230	+.0852	-.0505
(Line HN)	$\hat{g}_{HN,2}$	-1.2056	-.0620	-.0872
	$\hat{g}_{HN,1}$	+ .2084	+.0216	+.0629
	$\hat{g}_{HN,0}$	+ .9972	+.0404	+.0243
Hatch effect	$\hat{h}_1$	+2.5200	+.2612	+.1080
	$\hat{h}_2$	+2.3582	+.1470	-.0157
	$\hat{h}_3$	- .1489	+.0002	+.0372
	$\hat{h}_4$	+ .2686	-.0863	-.0618
	$\hat{h}_5$	-4.9979	-.3221	-.0677

The mean squares obtained for production periods 1 and 2 are given in Table 21.

No significant differences in production were obtained for genotypes or hatches but significant line differences were noted in both periods.

Egg production and egg weight for genotypes within line populations are presented in Table 22.

Table 18. Analyses of variance of body weights at three ages in Leghorn lines segregating for rose comb

Source	d.f.	Mean squares		
		8 week	Housing	December
Hatches	4	480.399[a]	3.234[a]	.455[b]
Lines	2	230.487[a]	7.120[a]	5.061[a]
Genotypes/lines	6	19.346	.217	.261
Error	490	44.862	.123	.153

[a]Significant at .01 level.

[b]Significant at .05 level.

Table 19. Body weights for Leghorn lines segregating for rose comb

Lines	Genotypes		
	RR	Rr^+	r^+r^+
Eight week weight (decigrams)			
9^4 x WL	57.9969	58.6388	58.2436
19^4 x WL	59.1724	50.1256	59.1654
HN^4 x WL	59.9278	61.3418	62.1306
Housing body weight (pounds)			
9^4 x WL	2.7756	2.8854	2.9366
19^4 x WL	2.9576	2.9544	3.0838
HN^4 x WL	3.2988	3.3824	3.4012
December body weight (pounds)			
9^4 x WL	3.6894	3.7318	3.5702
19^4 x WL	3.4853	3.4246	3.3792
HN^4 x WL	3.7567	3.9068	3.8682

Table 20. Parameter estimates for egg production and egg weight in Leghorn lines segregating for rose comb (see corresponding Appendix Tables 55-63)

Estimate		Period 1 (No. of eggs)	Period 2 (No. of eggs)	Egg weight (grams)
Pop. mean	$\hat{u}$	15.7332	8.3116	52.9187
Line effects	$\hat{l}_9$	-1.7318	-1.1598	-1.2888
	$\hat{l}_{19}$	- .0755	+ .5602	-1.7963
	$\hat{l}_{HN}$	+1.8073	+ .5996	+3.0851
Genotype effects (Line 9)	$\hat{g}_{9,2}$	-1.2610	+ .3124	+ .5173
	$\hat{g}_{9,1}$	+ .6804	+ .2353	- .3557
	$\hat{g}_{9,0}$	+ .5806	- .5477	- .1616
(Line 19)	$\hat{g}_{19,2}$	- .9775	- .1444	+ .0081
	$\hat{g}_{19,1}$	- .1533	+ .2646	+ .3629
	$\hat{g}_{19,0}$	+1.1308	- .1202	- .3710
(Line HN	$\hat{g}_{HN,2}$	+ .0913	+ .8802	+ .9862
	$\hat{g}_{HN,1}$	-1.2683	- .8287	- .1237
	$\hat{g}_{HN,0}$	+1.1770	- .0515	- .8625
Hatch effects	$\hat{h}_1$	+ .0997	- .5416	+1.5377
	$\hat{h}_2$	+ .1013	- .6407	+ .7572
	$\hat{h}_3$	+1.1536	- .2939	+ .0659
	$\hat{h}_4$	+ .6999	- .0851	- .3266
	$\hat{h}_5$	-2.0545	+1.5613	-2.0342

Table 21. Analyses of variance for egg production in the Leghorn lines segregating for rose comb

Source	Period 1 d.f.	Period 1 M.S.	Period 2 d.f.	Period 2 M.S.
Hatches	4	68.739	4	29.143
Lines	2	281.403[a]	2	113.619[a]
Genotypes/lines	6	62.791	6	11.596
Error	521	31.151	401	17.330

[a]Significant at .01 level.

Table 22. Egg production and egg weight means for the Leghorn lines segregating for rose comb

Lines	Genotypes RR	Rr^+	r^+r^+
Period 1 (No. of eggs)			
9^4_4 x WL	12.7305	14.6718	14.5720
19^4_4 x WL	14.6702	15.4944	16.7785
HN^4 x WL	17.6218	16.2622	18.7075
Period 2 (No. of eggs)			
9^4_4 x WL	7.4642	7.3871	6.6041
19^4_4 x WL	8.7274	9.1364	8.7516
HN^4 x WL	9.7914	8.0825	8.8597
Egg weight (grams)			
9^4_4 x WL	52.1472	51.2742	51.7915
19^4_4 x WL	51.1305	51.4853	40.7514
HN^4 x WL	56.9900	55.8801	55.1413

The mean squares obtained from the analysis of variance of egg weights are given in Table 23.

Table 23. Analysis of variance of egg weight in the Leghorn lines segregating for rose comb

Source	d.f.	M.S.
Hatches	4	97.613[a]
Lines	2	628.825[a]
Genotypes/lines	6	12.061
Error	407	16.737

[a]Significant at .01 level.

No significant differences were obtained for genotypes but there were significant differences existing between hatches and lines.

The line differences existing between the three Leghorn inbreds were: Line 9 being of small body size and low production, Line 19 of intermediate body size and production and Line HN being of larger body size and higher production.

Sex-linked barring

The sex-linked gene for barring (B) was segregating in one inbred line and no line (l) effect could be estimated. Also no evidence with respect to dominance was available.

Since (B) is sex-linked and only pullet data were analyzed, only two genetic classifications, barred (B-) and non-barred (b+) existed.

Body weight Parameter estimates obtained from the analyses of the three body weight measurements are presented in Table 24. The mean squares obtained from the body weight analyses are given in Table 25.

A significant difference is noted for bar vs. non-bar for eight week weight and was in favor of the non-bar individuals by 45.5 grams. At housing a difference in favor of the non-bar group of .17 pounds approached the .05 level of significance. The difference at December weight remained in favor of the non-bar group (.05 pounds) but did not approach significance. A significant mean square was noted

Table 24. Parameter estimates for body weight, egg production and egg weight for the barred Spanish line (see corresponding Appendix Tables 64-69)

Body weight		8 week (decigrams)	Housing (pounds)	December (pounds)
Pop. mean	$\hat{u}$	61.7934	3.2408	3.8504
Genotype effect	$\hat{B}ar$	-2.2767	-.0856	-.0240
	$\hat{N}on\text{-}bar$	+2.2767	+.0856	+.0240
Hatch effect	$\hat{h}_1$	+2.8413	+.2595	+.1435
	$\hat{h}_2$	-1.7880	-.0682	-.0839
	$\hat{h}_3$	- .0755	+.0824	+.1615
	$\hat{h}_4$	- .09878	-.2737	-.2211

Egg production (No. of eggs)		Period 1	Period 2
Pop. mean	$\hat{u}$	10.1296	6.6261
Genotype effect	$\hat{B}ar$	+ .2341	+.4750
	$\hat{N}on\text{-}bar$	- .2341	-.4750
Hatch effect	$\hat{h}_1$	+ .0036	+.4396
	$\hat{h}_2$	- .31740	-.3802
	$\hat{h}_3$	+2.5920	+1.5195
	$\hat{h}_4$	- .3216	-1.5789

Egg weight (Grams)		
Pop. mean	$\hat{u}$	56.5659
Genotype effect	$\hat{B}ar$	+ .2298
	$\hat{N}on\text{-}bar$	- .2298
Hatch effect	$\hat{h}_1$	- .0321
	$\hat{h}_2$	- .5276
	$\hat{h}_3$	+1.2712
	$\hat{h}_4$	- .7115

Table 25. Analyses of variance of body weight at three ages in the barred Spanish line

Source	d.f.	Mean squares		
		8 week	Housing	December
Hatches	3	130.641[a]	1.1514[a]	.6846[a]
Bar vs. Non-bar	1	626.770[a]	.7446	.0585
Error	101	57.920	.2084	.2212

[a]Significant at .01 level.

for hatches in all three periods.

No differences are noted between bar vs. non-bar with respect to egg production and egg weight. A significant hatch effect was obtained in period 1 egg production.

Egg production and egg weight Since all birds used in the production analyses had an egg weight record, the same coefficient matrix applies to both egg production periods and egg weight analyses.

Parameter estimates for egg production periods 1 and 2 and egg weight are presented in Table 24. The mean squares obtained for these traits are given in Table 26.

A summary of the means of the traits studied is presented in Table 27.

Table 26. Analyses of variance for egg production and egg weight in the barred Spanish line

Source	d.f.	Mean squares		Egg weight
		Period 1	Period 2	
Hatch	3	182.570[a]	20.728	11.324
Bar vs. non-bar	1	2.869	11.813	2.765
Error	49	41.110	19.964	16.553

[a]Significant at .01 level.

Table 27. Means of traits measured in Spanish line segregating for barring

Trait	Barred	Non-barred
Eight week weight (decigrams)	59.5167	64.0701
Housing weight (pounds)	3.1552	3.3264
December weight (pounds)	3.8264	3.8744
Egg production (1) (No. of eggs)	10.3637	9.8955
Egg production (2) (No. of eggs)	7.1011	6.1511
Egg weight (grams)	56.7957	56.3361

DISCUSSION

It is of interest and importance in a study of the kind just reported to consider the definition of the unit of heredity or gene in the light of modern molecular genetics as contrasted with classic or superficial genetic behavior.

First, a gene may be defined as a functional unit carrying the information necessary for the synthesis of a specific macromolecule. Several investigators, using bacteria and viruses, have established that the primary genetic information is carried in the form of desoxyribonucleic acid or DNA. In higher plants and animals the chromosomes are several orders of magnitude larger in cross-section area than are the DNA strands of bacterial viruses. Mazia (1954) presented evidence indicating that such chromosomes are made up of DNA-protein segments bound together, end to end, by divalent calcium and magnesium bridges. Units consisting of bundles of identical DNA segments, somehow combined with protein, could then correspond to the functional units of genetics.

Classically, the gene has been defined as a unit of recombination. However, increased resolving power by the use of microorganisms has shown that what was once thought to be a single mutant is in fact a group of mutational sites. To this group of mutational sites at which mutants are complementary to each other and show the so-called "cis-trans

effect" the name of cistron has been given (Pontecorvo, 1955). This revised definition of a functional unit no longer interprets the gene as an independent homogeneous unit, but rather an indefinitely limited part of a whole having a typical serial pattern which again is part of a larger pattern.

For the purpose of this study, an operational definition is suitable and represents the properties of the actual gene, so far as they may be established from experimental evidence by present methods.

Dominant White (I)

In the Spanish segregating lines, Sp^4 x 9 and Sp^4 x BA, I is an incomplete dominant, for all three genotypes were phenotypically distinguishable. In backcrossing to the Spanish line, heterozygotes became increasingly darker as the percentage of Spanish blood increased. This indicates a loss of dominance modifiers, since backcrossing to the Leghorn lines resulted in the complete dominant action of I.

One of the possible modifiers present in the Leghorn background is sex-linked barring (B). Hutt (1949) reported that B enhances the action of I. Evidence from crosses which involved the two Leghorn lines, 9 and BA, indicates that B is present in both lines. Recently, Van Albada (1960) reported the presence of a gene for sex-linked dilution of feather color in White Leghorns. Although no direct evidence was found that this gene was present, its action seems to

intensify whiteness in an already autosomal dominant white bird. Another dilution factor, blue plumage (Bl), was present in both Leghorn Lines 9 and BA and could account for some modifying action. Still another possible modifier would be the gene, silver (S), which was also present in both Leghorn lines.

In the Leghorn lines the segregation of white plumage due to I was masked by the presence of recessive white (c). However, the absence of black flecked birds in both segregating lines proved that I behaved as a complete dominant. Thus, the variable dominant action of the gene, I, in the two different genetic backgrounds leads to the question of, what is dominance.

According to the "presence and absence" hypothesis in vogue in early genetics, it was customary to refer to a dominant gene as present and to regard the recessive gene as merely the absence of the dominant. The discovery of multiple alleles showed that dominance and recessiveness could not be explained merely by the presence or absence of one entity. Genetically, however, whenever one allele is expressed to the exclusion of the other, it is said to be dominant over the other.

The variable dominance found in this study leads then to a biological definition of dominance. Goldschmidt (1955) states that dominance or recessivity is not the property of

a mutant locus, but a result of the action of the mutant locus in relation to the entire system of reactions constituting development. The variable dominance obtained also substantiates the conclusions of Fisher's (1938) study of dominance in the domestic fowl. He postulated that much of the dominance exhibited by mutant types is due to the selection of modifiers during the period of domestication which may raise deleterious mutants to a dominant position.

The I gene substitution in the genotypes Ii^+ or i^+i^+ had a different pigment effect which depended on genetic background. Also, growth depression was noted in cases in which I produced a distinct pigment effect, such as in the Spanish lines. No growth depression was found in the Leghorn lines where a small amount of pigment effect was produced. Also, as will be mentioned later, growth depression was also associated with the gene B, which also affects melanophore development. Hamilton (1940), in a study of the physiological properties of melanophores, reported that melanophores in the embryos of both dominant and recessive white breeds have a much lower viability and a higher sensitivity to adverse environmental conditions than melanophores of breeds having black plumage. Thus, if cell environment is influenced by the presence of I, growth depression is a possible result. In an already white or almost white breed a sub-optimal condition may already exist in the cells and the additional

effect of dominant white would not be expressed. This seemed especially true in the case of Line 9^4 x Sp, where the recessive white gene was present at a rather high frequency.

The interactions resulting in this growth depression do not support those results presented by Jaap and Grimes (1956). Their results indicated that growth supression resulted from the interaction of I with extension of black (E) and barring (B). Some additional depression was possible from the interaction with silver (S). In this study, growth depression was observed in the Spanish background in which only E was present, while no depression was observed in the Leghorn backgrounds in which all three genes, E, B, and S were present. Though no specific interactions could be demonstrated, it was observed that when I was introduced into a background in which it was not originally present, a growth suppression could be demonstrated.

Statistically significant differences were noted between the two genotypes II and Ii^+ in Line Sp^4 x 9 with respect to body weight. Since the difference was in favor of one genotype at one age and the other at another age, these differences are possibly due to the small number of homozygous dominant genotypes obtained in Line Sp^4 x 9. In the egg production analysis one statistically significant difference was noted in period 2, between genotypes II and Ii^+ within Line 9^4 x Sp. This difference could possibly be an effect of

the progeny testing that occurred in period 1, for no correction was applied to period 2 production.

The statistical model used in the analysis of metric traits included the effect of line. Since backcrossing was used to form the segregating lines, the two Spanish lines should differ not only by the allelic differences of the I gene, but also by the chromosomal portions of the two Leghorn ancestries remaining after three backcrosses. On the other hand, no differences were noted with respect to gene dominance or pleiotropic effects on body weight due to source of I from Line 9 or BA.

In case of body weight, a line difference was observed only at the eight week weigh period. This could be a heterotic effect resulting from residual chromosomal portions of the Leghorn lines, since growth rate to eight weeks of age appears to be a typical expression of hybrid vigor (Nordskog and Ghostley, 1954). The line differences obtained appear not to be due to an allelic difference but rather to additional genic material introduced on crossing. Furthermore, pen variation could possibly account for a portion of the line differences observed since lines were housed in different pens. Nordskog and Kempthorne (1959) reported that pen variation can account for eight and nine percent of the variation in egg production and egg weight, respectively.

Rose Comb (R)

No change in the complete dominance of the rose comb gene could be noted when it was introduced into three single comb inbred lines. However, alteration of the rose comb spike to a flattened blade in all three lines indicates that modifier genes also influence comb type.

Fisher's (1938) observation that the rose comb gene affected the frontal bone between the orbits seems to be substantiated in this study by the sudden appearance of cross-beak individuals when all three genotypes were produced. All but one of these cross-beak birds, classified with respect to genotype, were homozygous for rose comb. Thus, a possible difference between the two rose comb genotypes, (Rr^+) and (RR), is indicated. The incidence of cross-beak also suggests the presence of modifiers to normal rose combed varieties or breeds permitting normal skull development.

Sex-linked barring (B)

In this study a statistically significant difference at eight week weight of 45 grams in favor of non-barred females was noted. Nonsignificant differences persisted in favor of the non-barred pullets through the remaining weigh periods.

Mérat (1959c) observed barred and non-barred segregates in several populations and noted that body weights of non-barred females were significantly greater than barred females in some populations tested. Thus, the Spanish background

seems to be one in which the barring gene's action is not favorable to body growth. As in the case of dominant white, growth depression was observed when the gene in question actively affected melanophore development.

SUMMARY

Inbred lines segregating for a single locus were used to study the expression of dominance and the effects these genes have on other traits. The genes studied were: dominant white, rose comb and sex-linked barring. The economic traits measured were: body weight, egg production and egg weight.

Segregating inbred lines were produced by outcrossing an already established inbred line, to bring in a desired gene, and backcrossing the heterozygote in successive generations. This procedure kept the desired gene in the heterozygous condition and increased the percentage of blood of the inbred line in each successive backcross. In this study three backcrosses were made. Inter se matings of the heterozygotes produced the desired locus in all three genotypes. Progeny representing all genotypes were then performance tested.

Four lines were produced that were segregating for dominant white (I). The lines represented both parental backgrounds of a cross between Leghorn and Spanish lines. Two Leghorn parental lines were represented by the inbred Lines 9 and BA. The segregating genotypes of dominant white for each line were composed of 222 and 103 individuals, respectively. The two Spanish lines produced differed by the source, Line 9 or BA, of the introduced dominant allele. These segregating populations were represented by 260 and 254 individuals.

Differences in phenotypic expression for dominant white were noted in the parental backgrounds. In the Spanish background its action was that of incomplete dominance, for all three genotypes were phenotypically distinguishable. In the Leghorn backgrounds, dominant white was completely dominant, for it became necessary to progeny test to recessive testers after the second backcross generation in order to identify the heterozygote. In the segregating populations all females were progeny tested in order to classify all genotypes.

Of the metric traits measured, differences between genotypes were noted only with respect to body weight. In both Spanish lines, dominant white significantly depressed growth. In the two Leghorn lines no depression was observed. This type of gene action seems to support a modifying theory, for growth suppression varied as it did with respect to dominance with the particular background in which the gene was present. Evidence did seem to indicate that in cases in which dominant white produced a distinct pigment effect a growth depression was noted. When little or no pigment effect was observed no growth depression was found. This action supports a hypothesis that growth depression is possibly associated with melanophore development.

The rose comb gene (R) was introduced into three Leghorn inbred lines: 9, 19 and HN. After three backcross matings, inter se matings of heterozygotes produced progeny of all

three genotypes. These segregating populations for Lines 9, 19 and HN were represented by 293, 197 and 163 individuals, respectively.

Rose comb remained completely dominant in all three lines. All rose comb females were progeny tested to single comb males in order to distinguish homozygous (RR) and heterozygous (Rr^+) individuals. However, modification of the spike of the rose comb to that of a blade was observed. This modification indicates that there are modifiers of particular comb types.

No differences could be observed between the genotypes of rose comb with respect to any of the metric traits measured in any of the three lines.

The sex-linked barring gene (B) originated from a single barred male which appeared in the Spanish line. Inbreeding was practiced with planned heterozygosis at the barring locus. The segregating population in which the metric traits were measured was composed of 58 barred and 49 non-barred pullets, and their inbreeding coefficients ranged from 27 to 42 percent.

Since barring was segregating in but one line, no dominance difference could be tested. With respect to the metric traits measured, barred pullets were consistently lighter in body weight than non-barred pullets. No differences were noted in egg production and egg weight.

Here again, as in the case of dominant white, growth depression was observed when the gene in question actively affected melanophore action.

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APPENDIX

Table 28. Least-squares equations for body weights in Spanish lines segregating for dominant white

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{l}_{9}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{Ba-0}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{9-0}$	$\hat{h}_{1}$	$\hat{h}_{2}$	RHS		
												8 week	Housing	December
u	509	247	262	45	115	87	25	123	114	349	160	34081	1857.2	2056.9
l_{Ba}		247	0	45	115	87	0	0	0	182	65	16286	890.0	975.8
l_{9}			262	0	0	0	25	123	114	167	95	17795	967.2	1081.1
g_{Ba-2}				45	0	0	0	0	0	32	13	2901	159.6	171.2
g_{Ba-1}					115	0	0	0	0	84	31	7518	411.2	451.1
g_{Ba-0}						87	0	0	0	66	21	5867	319.2	353.3
g_{9-2}							25	0	0	21	4	1755	88.6	95.0
g_{9-1}								123	0	69	54	8098	446.0	506.0
g_{9-0}									114	77	37	7942	432.6	480.1
h_{1}										349	0	23776	1283.5	1402.9
h_{2}											160	10305	573.7	654.0

Table 29. Reduced normal equations for body weights in Spanish lines segregating for dominant white

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{h}_1$	RHS		
								8 week	Housing	December
u	509	-15	-42	28	-89	9	189	34081	1857.2	2056.9
l_{Ba}		509	-42	28	89	-9	45	-1509	-77.2	-105.3
g_{Ba-2}			132	87	0	0	-26	-2966	-159.6	-182.1
g_{Ba-1}				202	0	0	8	1651	92.0	97.8
g_{9-2}					139	114	-23	-6187	-344.0	-385.1
g_{9-1}						237	-25	156	13.4	25.9
h_1							509	13471	709.8	748.9

Table 30. Matrix inverse to reduced coefficient matrix for body weights in Spanish lines segregating for dominant white

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{h}_1$
u	.00318393	-.00036128	.00130295	-.00091286	.00380094	-.00206833	-.00099924
l_{Ba}		.00276272	.0013⁴316	-.00090753	-.003⁴7680	.00178080	-.00009687
g_{Ba-2}			.01212⁴53	-.00559288	-.0000309⁴	.0000274⁵	.00010463
g_{Ba-1}				.00761109	-.0000041⁰	.0000036⁴	.00001387
g_{9-2}					.01986113	-.00990308	-.0006⁹443
g_{9-1}						.00919406	.00061600
h_1							.0023⁴824

Table 31. Least-square equations for production (period 1) in Spanish lines segregating for dominant white

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{Ba}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{Ba-0}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{9-0}$	$\hat{h}_1$	$\hat{h}_2$	RHS
u	437	228	209	40	109	79	16	98	95	300	137	5929
l_9		228	0	40	109	79	0	0	0	175	53	3255
l_{Ba}			209	0	0	0	16	98	95	125	84	2674
g_{Ba-2}				40	0	0	0	0	0	29	11	538
g_{Ba-1}					109	0	0	0	0	82	27	1503
g_{Ba-0}						79	0	0	0	64	15	1214
g_{9-2}							16	0	0	12	4	189
g_{9-1}								98	0	49	49	1212
g_{9-0}									95	64	31	1273
h_1										300	0	4026
h_2											137	1903

Table 32. Reduced least-squares equations for production (period 1) in Spanish lines segregating for dominant white

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{h}$	RHS
u	437	19	-39	30	-79	3	163	5929
l_{Ba}		437	-39	30	79	-3	81	581
g_{Ba-2}			119	79	0	0	-31	-676
g_{Ba-1}				188	0	0	6	289
g_{9-2}					111	95	-25	-1084
g_{9-1}						193	-33	-61
h_1							437	2123

Table 33. Matrix inverse to reduced coefficient matrix for production (period 1) in Spanish lines segregating for dominant white

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{h}_1$
u	.00389909	-.00071163	.00148124	-.00109547	.00531514	-.00287869	-.00111565
l_{Ba}		.00350274	.00153783	-.00108010	-.00504070	.00248503	-.00036060
g_{Ba-2}			.01355274	-.00618353	-.00003918	.00005620	.00021076
g_{Ba-1}				.00826288	-.00001064	.00001527	.00005726
g_{9-2}					.02729710	-.01368676	-.00052278
g_{9-1}						.01212995	.00074990
h_1							.00281219

Table 34. Least-squares normal equations for production (period 2) in Spanish lines segregating for dominant white

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{l}_9$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{Ba-0}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{9-0}$	$\hat{h}_1$	$\hat{h}_2$	RHS
u	414	215	199	39	103	73	13	96	90	284	130	2602
l_{Ba}		215	0	39	103	73	0	0	0	166	49	1643
l_9			199	0	0	0	13	96	90	118	81	959
g_{Ba-2}				39	0	0	0	0	0	27	12	282
g_{Ba-1}					103	0	0	0	0	79	24	754
g_{Ba-0}						73	0	0	0	60	13	607
g_{9-2}							13	0	0	10	3	61
g_{9-1}								96	0	49	47	451
g_{9-0}									90	59	31	447
h_1										284	0	1853
h_2											130	749

Table 35. Reduced least-squares equations for production (period 2) in Spanish lines segregating for dominant white

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{h}_1$	RHS
u	414	16	-34	30	-77	6	154	2602
l_{Ba}		414	-34	30	77	-6	80	684
g_{Ba-2}			112	73	0	0	-32	-325
g_{Ba-1}				176	0	0	8	147
g_{9-2}					103	90	-21	-386
g_{9-1}						186	-26	4
h_1							414	1104

Table 36. Matrix inverse of reduced coefficient matrix for production (period 2) in Spanish lines segregating for dominant white

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{h}_1$
u	.00458639	-.00123314	.00138428	-.00109090	.00765067	-.00405829	-.00120648
l_{Ba}		.00413678	.00150185	-.00110227	-.00726580	.00364096	-.00034318
g_{Ba-2}			.01405202	-.00633877	-.00010063	.00010913	.00040525
g_{Ba-1}				.00868658	.00000973	-.00001055	-.00003919
g_{9-2}					.03676350	-.01837375	-.00073889
g_{9-1}						.01462700	.00080130
h_1							.00297548

Table 37. Least-squares equations for egg weight in Spanish lines segregating for dominant white

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{l}_9$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{Ba-0}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{9-0}$	$\hat{h}_1$	$\hat{h}_2$	RHS
u	260	140	120	23	63	54	9	58	53	168	92	15412
l_{Ba}		140	0	23	63	54	0	0	0	104	36	8366
l_9			120	0	0	0	9	58	53	64	56	7046
g_{Ba-2}				23	0	0	0	0	0	14	9	1383
g_{Ba-1}					63	0	0	0	0	46	17	3767
g_{Ba-0}						54	0	0	0	44	10	3216
g_{9-2}							9	0	0	6	3	527
g_{9-1}								58	0	25	33	3393
g_{9-0}									53	33	20	3126
h_1										168	0	9966
h_2											92	5446

Table 38. Reduced least-squares equations for egg weight in Spanish lines segregating for dominant white

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{n}_1$	RHS
u	260	20	-31	9	-44	5	76	15412
l_{Ba}		260	-39	9	44	-5	60	1320
g_{Ba-2}			77	54	0	0	-29	-1833
g_{Ba-1}				117	0	0	-5	551
g_{9-2}					62	53	-10	-2599
g_{9-1}						111	-21	267
h_1							260	4520

Table 39. Inverse matrix of reduced coefficient matrix of egg weight in Spanish lines segregating for dominant white

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{h}_1$
u	.0064031	-.00173413	.00262957	-.00164793	.01058778	-.00568449	-.00133113
l_{Ba}		.00634783	.00277615	-.00166440	-.01021656	.00511737	-.00065996
g_{Ba-2}			.02336287	-.01115604	-.00018603	.00028421	.00099782
g_{Ba-1}				.01394596	.00002090	-.00003193	-.00011212
g_{9-2}					.05355367	-.02666896	-.00085184
g_{9-1}						.02247562	.00130138
h_1							.00456904

Table 40. Least-squares normal equations for body weights in Leghorn lines segregat

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{Ba}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{9-0}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}$
u	242	169	73	29	98	42	17	30	
l_9		169	0	29	98	42	0	0	
l_{Ba}			73	0	0	0	17	30	
g_{9-2}				29	0	0	0	0	
g_{9-1}					98	0	0	0	
g_{9-0}						42	0	0	
g_{Ba-2}							17	0	
g_{Ba-1}								30	
g_{Ba-0}									
h_1									
h_2									
h_3									
h_4									
h_5									

r body weights in Leghorn lines segregating for dominant white

$\hat{g}_{9-1}$	$\hat{g}_{9-0}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{Ba-0}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	$\hat{h}_5$
98	42	17	30	26	68	49	55	40	30
98	42	0	0	0	65	23	28	27	26
0	0	17	30	26	3	26	27	13	4
0	0	0	0	0	12	4	7	4	2
98	0	0	0	0	38	14	16	15	15
	42	0	0	0	15	5	5	8	9
		17	0	0	0	6	7	4	0
			30	0	2	14	9	5	0
				26	1	6	11	4	4
					68	0	0	0	0
						49	0	0	0
							55	0	0
								40	0
									30

dominant white

$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	$\hat{h}_5$	RHS		
					8 week	Housing	December
68	49	55	40	30	14283	725.4	893.3
65	23	28	27	26	9919	476.2	604.9
3	26	27	13	4	4364	249.2	288.4
12	4	7	4	2	1668	81.1	105.6
38	14	16	15	15	5795	277.1	349.7
15	5	5	8	9	2456	118.0	149.6
0	6	7	4	0	990	56.1	65.2
2	14	9	5	0	1794	103.1	119.0
1	6	11	4	4	1580	90.0	104.2
68	0	0	0	0	4038	210.1	248.8
	49	0	0	0	2980	152.4	182.4
		55	0	0	3255	170.5	210.8
			40	0	2357	116.2	144.2
				30	1653	76.2	107.1

Table 41. Reduced least-squares equations for body weights in Leghorn lines segregating for dominant white

	$\hat{u}$	$\hat{l}_9$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	RHS		
											8 weeks	Housing	December
u	242	96	-13	56	- 9	4	38	19	25	10	14283	725.4	893.3
l_9		242	-13	56	9	- 4	40	-25	-21	- 8	5555	227.0	316.5
g_{9-2}			71	42	0	0	4	6	9	3	-788	-36.9	-44.0
g_{9-1}				140	0	0	17	3	5	1	3339	159.1	200.1
g_{Ba-2}					43	26	3	4	0	4	-590	-33.9	-39.0
g_{Ba-1}						56	5	12	2	5	214	13.1	14.8
h_1							48	30	30	30	2385	133.9	141.7
h_2								79	30	30	1327	76.2	75.3
h_3									85	30	1602	94.3	103.7
h_4										70	704	40.0	37.1

Table 42. Matrix inverse to reduced coefficient matrix for body weights in Leghorn line

	$\hat{u}$	$\hat{l}_9$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{Ba-2}$
u	.00608812	-.00218515	.00234589	-.00213501	.00276086
l_9		.00673319	.00171276	-.00208207	-.00286901
g_{9-2}			.01942209	-.00731369	.00014559
g_{9-1}				.01101978	-.00003088
g_{Ba-2}					.03432918
g_{Ba-1}					
h_1					
h_2					
h_3					
h_4					

lines segregating for dominant white

2	$\hat{g}_{Ba-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$
086	-.00149709	-.00026636	-.00145583	-.00192398	.00032232
901	.00155680	-.00323923	.00276059	.00226481	.00032525
559	.00008176	-.00057598	-.00051468	-.00160699	.00027470
088	.00002975	-.00001746	-.00017062	.00023370	.00020316
918	-.01618698	.00061475	-.00028510	-.00079977	-.00133207
	.02614312	-.00055130	-.00267965	.00123329	.00030161
		.01498212	-.00393213	-.00326201	-.00364067
			.01840971	-.00229606	-.00446499
				.01642664	-.00410113
					.01954822

Table 43. Least-squares equations for production (period 1) in Leghorn lines segregating for dominant white

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{Ba}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{9-0}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{Ba-0}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	$\hat{h}_5$	RHS
u	261	187	74	37	98	52	21	30	23	73	55	57	44	32	4002
l_9		187	0	37	98	52	0	0	0	70	27	32	29	29	2623
l_{Ba}			74	0	0	0	21	30	23	3	28	25	15	3	1379
g_{9-2}				37	0	0	0	0	0	13	7	10	5	2	498
g_{9-1}					98	0	0	0	0	38	14	16	15	15	1432
g_{9-0}						52	0	0	0	19	6	6	9	12	693
g_{Ba-2}							21	0	0	0	8	7	6	0	400
g_{Ba-1}								30	0	2	14	9	5	0	578
g_{Ba-0}									23	1	6	9	4	3	401
h_1										73	0	0	0	0	1133
h_2											55	0	0	0	906
h_3												57	0	0	925
h_4													44	0	672
h_5														32	366

Table 44. Reduced least-squares equations for production (period 1) in Leghorn lines segregating for dominant white

	$\hat{u}$	$\hat{l}_9$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	RHS
u	261	113	-15	46	-2	7	41	23	25	12	4002
l_9		261	-15	46	2	-7	41	-27	-19	-12	1244
g_{9-2}			89	52	0	0	4	11	14	6	-195
g_{9-1}				150	0	0	16	5	7	3	739
g_{Ba-2}					44	23	2	5	1	5	-1
g_{Ba-1}						53	4	11	3	4	77
h_1							105	32	32	32	767
h_2								87	32	32	540
h_3									89	32	559
h_4										76	306

Table 45. Inverse matrix to reduced coefficient matrix for production (period 1) for

	$\hat{u}$	$\hat{l}_9$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{Ba}$
u	.00557519	-.00235173	.00187965	-.00149982	.0011
l_9		.00603413	.00088372	-.00131534	-.0012
g_{9-2}			.01578488	-.00620949	.0001
g_{9-1}				.00969226	-.0000
g_{Ba-2}					.0299
g_{Ba-1}					
h_1					
h_2					
h_3					
h_4					

for Leghorn lines segregating for dominant white

$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$
0116522	-.00111076	-.00010099	-.00167841	-.00160550	.00006622
0129070	.00120615	-.00280566	.00250819	.00173416	.00072274
0012580	.00016690	.00022225	-.00127623	-.00200209	.00011139
0002568	-.00000221	-.00032628	.00018028	.00039581	.00003338
2992986	-.01315108	.00062656	-.00036272	.00003913	-.00180117
	.02526268	-.00050818	-.00206637	.00048987	.00076608
		.01375368	-.00349183	-.00299960	-.00350398
			.01658021	-.00209318	-.00374226
				.01550006	-.00374062
					.01795567

Table 46. Least-squares equations for production (period 2) in Leghorn lines segregating for dominant white

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{l}_9$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{Ba-0}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{9-0}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	$\hat{h}_5$	RHS
u	200	52	148	14	20	18	25	91	32	56	41	47	31	25	1568
l_{Ba}		52	0	14	20	18	0	0	0	2	21	20	7	2	571
l_9			148	0	0	0	25	91	32	54	20	27	24	23	997
g_{Ba-2}				14	0	0	0	0	0	0	6	4	4	0	180
g_{Ba-1}					20	0	0	0	0	1	10	8	1	0	218
g_{Ba-0}						18	0	0	0	1	5	8	2	2	173
g_{9-2}							25	0	0	12	3	5	3	2	207
g_{9-1}								91	0	33	13	17	15	13	539
g_{9-0}									32	9	4	5	6	8	251
h_1										56	0	0	0	0	390
h_2											41	0	0	0	360
h_3												47	0	0	391
h_4													31	0	245
h_5														25	182

Table 47. Reduce least-squares equations for production (period 2) of Leghorn lines segregating for dominant white

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	RHS
u	200	-96	-4	2	-7	59	31	16	22	6	1568
l_{Ba}		200	-4	2	7	-59	-31	22	14	4	-426
g_{Ba-2}			32	18	0	0	1	3	-2	4	7
g_{Ba-1}				38	0	0	2	7	2	1	45
g_{9-2}					57	32	9	5	6	3	-44
g_{9-1}						123	19	4	7	4	288
h_1							81	25	25	25	208
h_2								66	25	25	178
h_3									72	25	209
h_4										56	63

Table 48. Inverse matrix to the reduced coefficient matrix for production (period 2) in Leghorn

	$\hat{u}$	$\hat{l}_{Ba}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{9-2}$
u	.00802946	.00342097	.00190150	-.00092720	.00250448
l_{Ba}		.00885531	.00215667	-.00094324	-.00223832
g_{Ba-2}			.04436741	-.02119097	-.00016611
g_{Ba-1}				.03700824	.00025345
g_{9-2}					.02298365
g_{9-1}					
h_1					
h_2					
h_3					
h_4					

n Leghorn lines segregating for dominant white

	$\hat{g}_{9-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$
448	-.00264069	-.00024991	-.00252741	-.00242859	.00115460
832	.00289792	.00371827	-.00426525	-.00265845	.00020765
611	.00006129	.00087603	-.00046947	.00218001	-.00429867
345	.00004243	-.00035884	-.00304927	-.00102760	.00298312
365	-.00784642	-.00245440	-.00019378	-.00084864	.00078916
	.01282217	.00025784	-.00044266	-.00019624	-.00025416
		.01802493	-.00481290	-.00344290	-.00454313
			.02261939	-.00220990	-.00622152
				.01928956	-.00567983
					.02528958

Table 49. Least-squares equations for egg weight in Leghorn lines segregating for dominant white

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{Ba}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{9-0}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{g}_{Ba-0}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	$\hat{h}_5$	RHS
u	194	133	61	25	75	33	16	26	19	51	42	44	34	23	9705
l_9		133	0	25	75	33	0	0	0	49	18	23	23	20	6461
l_{Ba}			61	0	0	0	16	26	19	2	24	21	11	3	3244
g_{9-2}				25	0	0	0	0	0	10	3	6	4	2	1226
g_{9-1}					75	0	0	0	0	29	11	12	12	11	3650
g_{9-0}						33	0	0	0	10	4	5	7	7	1585
g_{Ba-2}							16	0	0	0	6	6	4	0	864
g_{Ba-1}								26	0	1	13	8	4	0	1376
g_{Ba-0}									19	1	5	7	3	3	1004
h_1										51	0	0	0	0	2546
h_2											42	0	0	0	2177
h_3												44	0	0	2262
h_4													34	0	1645
h_5														23	1075

Table 50. Reduced least-squares equations for egg weight in Leghorn lines segregating for dominant white

	$\hat{u}$	$\hat{l}_9$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{Ba-2}$	$\hat{g}_{Ba-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	RHS
u	194	72	-8	42	-3	7	28	19	21	11	9705
l_9		194	-8	42	3	-7	30	-23	-15	-5	3217
g_{9-2}			58	33	0	0	5	4	6	2	-359
g_{9-1}				108	0	0	15	3	3	1	2065
g_{Ba-2}					35	19	2	4	2	4	-140
g_{Ba-1}						45	3	11	4	4	372
h_1							74	23	23	23	1471
h_2								65	23	23	1102
h_3									67	23	1187
h_4										57	570

Table 51. Inverse matrix to reduced coefficient matrix for egg weight in Leghorn lines segr

	$\hat{u}$	$\hat{l}_9$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{Ba-2}$
u	.00729115	-.00259445	.00241290	-.00243929	.00215131
l_9		.00807974	.00189641	-.00233344	-.00220489
g_{9-2}			.02293541	-.00849570	.00013964
g_{9-1}				.01377865	-.00006623
g_{Ba-2}					.03818591
g_{Ba-1}					
h_1					
h_2					
h_3					
h_4					

ɜ segregating for dominant white

-2	$\hat{g}_{Ba-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$
5131	-.00172641	-.00002768	-.00215826	-.00220641	.00006602
0489	.00165840	-.00402550	.00391937	.00246752	.00026934
3964	.00010870	-.00099277	-.00020398	-.00155807	.00018355
6623	.00008904	-.00054480	-.00040816	.00054286	.00048630
3591	-.01654516	.00065406	-.00020966	-.00079984	-.00198754
	.03047589	-.00015951	-.00345992	.00056574	.00072786
		.01963951	-.00522733	-.00420707	-.00445594
			.02249299	-.00242190	-.00495744
				.02019658	-.00476696
					.02335007

Table 52. Least-squares equations for body weights in Leghorn lines segregating for rose

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{19}$	$\hat{l}_{HN}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{9-0}$	$\hat{g}_{19-2}$	$\hat{g}_{19-1}$	$\hat{g}_{19-0}$	$\hat{g}_{HN-}$
u	503	218	155	130	47	109	52	35	84	36	20
l_9		218	0	0	47	109	62	0	0	0	0
l_{19}			155	0	0	0	0	35	84	36	0
l_{HN}				130	0	0	0	0	0	0	20
g_{9-2}					47	0	0	0	0	0	0
g_{9-1}						109	0	0	0	0	0
g_{9-0}							62	0	0	0	0
g_{19-2}								35	0	0	0
g_{19-1}									84	0	0
g_{19-0}										36	0
g_{HN-2}											20
g_{HN-1}											
g_{HN-0}											
h_1											
h_2											
h_3											
h_4											
h_5											

rose comb

$\hat{g}_{HN-2}$	$\hat{g}_{HN-1}$	$\hat{g}_{HN-0}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	$\hat{h}_5$	RHS		
								8 weeks	housing	December
20	64	46	200	101	120	47	35	30521	1579.3	1854.9
0	0	0	110	40	68	0	0	13090	661.7	815.3
0	0	0	57	27	32	24	15	9382	468.4	535.5
20	64	46	33	34	20	23	20	8049	449.2	504.1
0	0	0	21	12	14	0	0	2805	137.7	176.0
0	0	0	50	22	37	0	0	6564	330.8	413.2
0	0	0	39	6	17	0	0	3721	193.2	226.1
0	0	0	14	5	8	4	4	2098	104.9	123.2
0	0	0	31	14	12	16	11	5103	249.8	289.1
0	0	0	12	8	12	4	0	2181	113.7	123.2
20	0	0	4	3	4	7	2	1207	67.0	75.1
	64	0	20	19	7	11	7	3988	223.8	251.0
		46	9	12	9	5	11	2854	158.4	178.0
			200	0	0	0	0	12352	649.8	748.3
				101	0	0	0	6275	325.3	270.5
					120	0	0	7087	358.7	441.6
						47	0	2852	144.6	167.9
							35	1955	100.9	126.6

Table 53. Reduced least-squares equations for body weights in Leghorn lines segregating for rose comb

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{19}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{19-2}$	$\hat{g}_{19-1}$	$\hat{g}_{HN-2}$	$\hat{g}_{HN-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	RHS		
														8 weeks	Housing	December
u	503	88	25	-15	47	- 1	48	-26	18	165	66	85	12	30521	1579.3	1854.9
l_9		248	130	-15	47	0	0	25	-18	97	26	68	- 3	5041	212.5	311.2
l_{19}			285	0	0	- 1	48	26	-18	29	- 2	17	6	1333	19.2	31.4
g_{9-2}				109	62	0	0	0	0	-18	6	- 3	0	-916	-55.5	-50.1
g_{9-1}					171	0	0	0	0	11	16	20	0	2843	137.6	187.1
g_{19-2}						71	36	0	0	- 2	- 7	- 8	- 4	-83	-8.8	0
g_{19-1}							120	0	0	8	- 5	-11	1	2922	136.1	165.9
g_{HN-2}								66	46	4	0	4	11	-1647	-91.4	-102.9
g_{HN-1}									110	15	11	2	10	1134	65.4	73.0
h_1										235	35	35	35	10397	548.9	621.7
h_2											136	35	35	4320	224.4	243.9
h_3												155	35	5132	257.8	315.0
h_4													82	897	43.7	41.3

Table 54. Matrix inverse of reduced coefficient matrix for body weights in Leghorn lines

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{19}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{19-2}$	
u	.00339763	-.00000108	-.00004320	.00056512	-.00084384	.00060013	-.0
l_9		.00496162	-.00183731	.00120420	-.00143340	-.00063425	.0
l_{19}			.00504210	-.00065194	.00070299	.00129289	-.0
g_{9-2}				.01234157	-.00494635	-.00003483	.0
g_{9-1}					.00826172	-.00001669	-.0
g_{19-2}						.01716937	-.0
g_{19-1}							.0
g_{HN-2}							
g_{HN-1}							
h_1							
h_2							
h_3							
h_4							

nes segregating for rose comb

$\hat{g}_{19-1}$	$\hat{g}_{HN-2}$	$\hat{g}_{HN-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$
-.00157375	.00218440	-.00119706	-.00203631	-.00094718	-.00149705	.00131975
.00084540	-.00259443	.00173669	-.00173580	-.00068608	-.00163113	.00214105
-.00236861	-.00223434	.00145693	.00012426	.00030818	.00011472	-.00044934
.00000320	-.00004809	.00001709	.00043018	-.00063812	.00014844	.00003708
-.00002901	.00000432	-.00002821	.00031626	-.00013376	-.00025465	.00003816
-.00587965	-.00009991	-.00002318	-.00012765	.00038384	.00009396	.00057038
.01178884	.00009045	-.00008081	.00047995	.00050246	.00128380	-.00096560
	.02697657	-.01231966	.00042243	.00106637	-.00000974	-.00300478
		.01510164	-.00077398	-.00094201	.00009942	.00063294
			.00671981	.00015116	.00101002	-.00311280
				.00913105	-.00042801	-.00370385
					.00885523	-.00389897
						.01705243

Table 55. Least-squares equations for production (period 1) of Leghorn lines segregati

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{19}$	$\hat{l}_{HN}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{9-0}$	$\hat{g}_{19-2}$	$\hat{g}_{19-1}$
u	510	217	161	132	52	111	54	41	87
l_9		217	0	0	52	111	54	0	0
l_{19}			161	0	0	0	0	41	87
l_{HN}				132	0	0	0	0	0
g_{9-2}					52	0	0	0	0
g_{9-1}						111	0	0	0
g_{9-0}							54	0	0
g_{19-2}								41	0
g_{19-1}									87
g_{19-0}									
g_{HN-2}									
g_{HN-1}									
g_{HN-0}									
h_1									
h_2									
h_3									
h_4									
h_5									

ating for rose comb

$\hat{g}_{19-0}$	$\hat{g}_{HN-2}$	$\hat{g}_{HN-1}$	$\hat{g}_{HN-0}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	$\hat{h}_5$	RHS
33	25	65	42	200	110	118	47	35	7996
0	0	0	0	103	44	70	0	0	3172
33	0	0	0	63	29	31	24	14	2541
0	25	65	42	34	37	17	23	21	2283
0	0	0	0	21	16	15	0	0	1679
0	0	0	0	50	22	39	0	0	1679
0	0	0	0	32	6	16	0	0	810
0	0	0	0	18	7	9	4	3	611
0	0	0	0	34	14	12	16	11	1363
33	0	0	0	11	8	10	4	0	567
	25	0	0	6	5	4	7	3	445
		65	0	20	20	6	12	7	1062
			42	8	12	7	4	11	776
				200	0	0	0	0	3045
					110	0	0	0	1717
						118	0	0	1917
							47	0	801
								35	516

Table 56. Reduced least-squares equations for production (period 1) in Leghorn lines segregating for rose comb

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{19}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{19-2}$	$\hat{g}_{19-1}$	$\hat{g}_{HN-2}$	$\hat{g}_{HN-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	RHS
u	510	85	29	-2	57	8	54	-17	23	165	75	83	12	7996
l_9		349	132	-2	57	0	0	17	-23	90	28	74	-2	889
l_{19}			293	0	0	8	54	17	-23	36	-1	21	8	258
g_{9-2}				106	54	0	0	0	0	-11	10	-1	0	-127
g_{9-1}					165	0	0	0	0	18	16	23	0	869
g_{19-2}						74	33	0	0	4	-4	-4	-3	44
g_{19-1}							120	0	0	12	-5	-9	1	796
g_{HN-2}								67	42	6	1	5	11	-331
g_{HN-1}									107	16	12	3	12	286
h_1										235	35	35	35	2529
h_2											145	35	35	1201
h_3												153	35	1401
h_4													82	285

Table 57. Inverse matrix to the reduced coefficient matrix for production (period 1) for

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{19}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{19-2}$	$\hat{g}_{19}$
u	.00330578	.00009270	.00006356	.00033045	-.00074671	.00037019	-.0015
l_9		.00477226	-.00184650	.00071604	-.00144394	-.00013803	.0008
l_{19}			.00485243	-.00043783	.00072866	.00040247	-.0023
g_{9-2}				.01174178	-.00422067	-.00004284	-.0000
g_{9-1}					.00821740	-.00000625	-.0000
g_{19-2}						.01553528	-.0046
g_{19-1}							.0114
g_{HN-2}							
g_{HN-1}							
h_1							
h_2							
h_3							
h_4							

for Leghorn lines segregating for rose comb

$\hat{g}_{19-1}$	$\hat{g}_{HN-2}$	$\hat{g}_{HN-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$
.00158535	.00145391	-.00093899	-.00202136	-.00115966	-.00145268	.00146534
.00080026	-.00162287	.00137080	-.00148772	-.00063362	-.00177395	.00194789
.00232274	-.00142546	.00123318	-.00005850	.00029153	.00006218	-.00059629
.00000342	-.00006196	.00002143	.00051164	-.00086708	.00032036	.00003044
.00002884	.00001131	.00002782	.00017283	.00008429	-.00032817	.00003597
.00463924	-.00007440	.00000267	-.00040835	.00006929	-.00015854	.00074036
.01145035	.00003634	-.00004199	.00049993	.00071227	.00127384	-.00088377
	.02242323	-.00963295	.00010888	.00067453	-.00007140	-.00201865
		.01407931	-.00063967	-.00068838	.00005858	-.00017456
			.00655196	.00024442	.00095766	-.00298646
				.00861524	-.00030920	-.00351967
					.00906417	-.00400271
						.01690605

Table 58. Least-squares equations for production (period 2) for Leghorn lines segregating

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{19}$	$\hat{l}_{HN}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{9-0}$	$\hat{g}_{19-2}$	$\hat{g}_{19-1}$	$\hat{g}_{1}$
u	414	177	128	109	40	88	49	29	69	3
l_9		177	0	0	40	88	49	0	0	
l_{19}			128	0	0	0	0	29	69	3
l_{HN}				109	0	0	0	0	0	
g_{9-2}					40	0	0	0	0	
g_{9-1}						88	0	0	0	
g_{9-0}							49	0	0	
g_{19-2}								29	0	
g_{19-1}									69	
g_{19-0}										3
g_{HN-2}										
g_{HN-1}										
g_{HN-0}										
h_1										
h_2										
h_3										
h_4										
h_5										

ing for rose comb

$\hat{g}_{19-0}$	$\hat{g}_{HN-2}$	$\hat{g}_{HN-1}$	$\hat{g}_{HN-0}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	$\hat{h}_5$	RHS
30	18	56	35	156	89	101	37	31	3231
0	0	0	0	82	34	61	0	0	1188
30	0	0	0	46	24	26	17	15	1120
0	18	56	35	28	31	14	20	16	923
0	0	0	0	16	11	13	0	0	279
0	0	0	0	36	18	34	0	0	609
0	0	0	0	30	5	14	0	0	300
0	0	0	0	11	5	7	2	4	259
0	0	0	0	27	12	10	9	11	616
30	0	0	0	8	7	9	6	0	245
	18	0	0	4	3	4	6	1	172
		56	0	16	18	5	10	7	441
			35	8	10	5	4	8	310
				156	0	0	0	0	1151
					89	0	0	0	669
						101	0	0	766
							37	0	324
								31	321

Table 59. Reduced least-squares equations for production (period 2) in Leghorn lines segregating for rose comb

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{19}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{19-2}$	$\hat{g}_{19-1}$	$\hat{g}_{HN-2}$	$\hat{g}_{HN-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	RHS
u	414	68	19	-9	39	-1	39	-17	21	125	58	70	6	3231
l_9		286	109	-9	39	0	0	17	-21	70	19	63	-4	265
l_{19}			237	0	0	-1	39	17	-21	19	-6	13	-2	197
g_{9-2}				89	49	0	0	0	0	-14	6	-1	0	-21
g_{9-1}					137	0	0	0	0	6	13	20	0	309
g_{19-2}						59	30	0	0	-1	-6	-6	-8	14
g_{19-1}							99	0	0	8	-6	-10	-8	371
g_{HN-2}								53	35	3	0	6	9	-138
g_{HN-1}									91	9	9	1	7	131
h_1										187	31	31	31	830
h_2											120	31	31	348
h_3												132	31	445
h_4													68	3

Table 60. Inverse matrix to the reduced coefficient matrix for production (period 2) in Legh

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{19}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{19-2}$	$\hat{g}_{19}$
u	.00397448	.00001781	-.00010817	.00059188	-.00087765	.00066978	-.0016
l_9		.00598086	-.00232346	.00124739	-.00167884	-.00061408	.0012
l_{19}			.00606007	-.00068915	.00083840	.00155878	-.0028
g_{9-2}				.01475617	-.00577601	-.00006463	-.0000
g_{9-1}					.01015428	.00002585	-.0000
g_{19-2}						.02076255	-.0070
g_{19-1}							.0141
g_{HN-2}							
g_{HN-1}							
h_1							
h_2							
h_3							
h_4							

eghorn lines segregating for rose comb

$\hat{g}_{19-1}$	$\hat{g}_{HN-2}$	$\hat{g}_{HN-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$
)165095	.00241412	-.00163961	-.00226677	-.00120605	-.00175920	.00176620
)120264	-.00250554	.00187976	-.00193723	-.00068566	-.00222657	.00270005
)281561	-.00237486	.00176070	.00027688	.00042827	.00032559	-.00043359
)002068	-.00007712	.00004269	.00060203	-.00084915	.00019781	.00001914
)008196	.00003838	-.00004259	.00046573	-.00008172	-.00050705	.00005214
)701588	-.00040856	.00009583	-.00025728	.00020076	-.00018065	.00025173
415646	-.00019252	.00000592	-.00001569	.00046521	.00118865	.00025173
	.03066814	-.01333404	.00022132	.00109728	-.00067530	-.00348062
		.01740954	-.00044627	-.00089418	.00043398	.00070489
			.00810580	.00005182	.00106717	-.00412669
				.01046495	-.00048875	-.00446775
					.01075849	-.00497118
						.02150054

Table 61. Least-squares equations for egg weight in Leghorn lines segregating for rose comb

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{19}$	$\hat{l}_{HN}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{9-0}$	$\hat{g}_{19-2}$	$\hat{g}_{19-1}$	$\hat{g}_{19-0}$
u	420	183	129	108	44	92	47	32	70	27
l_9		183	0	0	44	92	47	0	0	0
l_{19}			129	0	0	0	0	32	70	27
l_{HN}				108	0	0	0	0	0	0
g_{9-2}					44	0	0	0	0	0
g_{9-1}						92	0	0	0	0
g_{9-0}							47	0	0	0
g_{19-2}								32	0	0
g_{19-1}									70	0
g_{19-0}										27
g_{HN-2}										
g_{HN-1}										
g_{HN-0}										
h_1										
h_2										
h_3										
h_4										
h_5										

ose comb

$\hat{g}_{19-0}$	$\hat{g}_{HN-2}$	$\hat{g}_{HN-1}$	$\hat{g}_{HN-0}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	$\hat{h}_5$	RHS
27	16	53	39	161	90	96	40	33	22307
0	0	0	0	86	37	60	0	0	9595
27	0	0	0	47	24	23	21	14	6667
0	16	53	39	28	29	13	19	19	6045
0	0	0	0	19	12	13	0	0	2333
0	0	0	0	40	20	32	0	0	4796
0	0	0	0	27	5	15	0	0	2466
0	0	0	0	13	5	5	5	4	1650
0	0	0	0	27	13	9	11	10	3632
27	0	0	0	7	6	9	5	0	1385
	16	0	0	4	2	3	5	2	914
		53	0	17	15	5	10	6	2984
			39	7	12	5	4	11	2147
				161	0	0	0	0	8653
					90	0	0	0	4820
						96	0	0	4999
							40	0	2127
								33	1708

Table 62. Reduced least-squares equations for egg weight in Leghorn lines segregating for rose comb

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{19}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{19-2}$	$\hat{g}_{19-1}$	$\hat{g}_{HN-2}$	$\hat{g}_{HN-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	RHS
u	420	75	21	-3	45	5	43	-23	14	128	57	63	7	22307
l_9		291	108	-3	45	0	0	23	-14	77	27	66	0	3550
l_{19}			237	0	0	5	43	23	-14	24	0	15	7	622
g_{9-2}				91	47	0	0	0	0	-8	7	-2	0	-133
g_{9-1}					139	0	0	0	0	13	15	17	0	2330
g_{19-2}						59	27	0	0	2	-5	-8	-4	265
g_{19-1}							97	0	0	10	-3	-10	-4	2247
g_{HN-2}								55	39	6	-1	7	10	-1233
g_{HN-1}									92	15	8	5	11	837
h_1										194	33	33	33	6945
h_2											123	33	33	3112
h_3												129	33	3291
h_4													73	419

Table 63. Inverse matrix of reduced coefficient matrix for egg weight in Leghorn lines segre

	$\hat{u}$	$\hat{l}_9$	$\hat{l}_{19}$	$\hat{g}_{9-2}$	$\hat{g}_{9-1}$	$\hat{g}_{19-2}$	$\hat{g}_{19}$
u	.00386566	-.00013811	-.00009374	.00042750	-.00086305	.00033012	-.0016
l_9		.00605164	-.00226671	.00089475	-.00165739	-.00051094	.0012
l_{19}			.00613884	-.00050001	.00081872	.00083438	-.0029
g_{9-2}				.01375862	-.00507935	.00002771	.0000
g_{9-1}					.00974509	-.00003713	-.0000
g_{19-2}						.01969491	-.0058
g_{19-1}							.0141
g_{HN-2}							
g_{HN-1}							
h_1							
h_2							
h_3							
h_4							

egregating for rose comb

$\hat{g}_{19-1}$	$\hat{g}_{HN-2}$	$\hat{g}_{HN-1}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$
00166646	.00292733	-.00152624	-.00212763	-.00101636	-.00146847	.00147915
00124812	-.00313952	.00212016	-.00192239	-.00084137	-.00236312	.00269922
00293047	-.00283750	.00183426	.00026104	.00039948	.00038427	-.00105452
00001372	-.00010946	.00002109	.00039894	-.00077261	.00036920	.00002002
00003281	-.00000989	-.00002308	.00033095	-.00017145	-.00024407	.00004348
00588021	-.00006873	-.00003880	-.00024528	.00043983	.00065830	.00027503
01411503	-.00014643	-.00006165	.00003281	.00021973	.00111870	.00030150
	.03329699	-.01525721	.00012274	.00142313	-.00040441	-.00279861
		.01837970	-.00086789	-.00086165	-.00001777	.00007532
			.00781266	.00004189	.00090032	-.00367637
				.01026554	-.00063942	-.00434255
					.01098864	-.00482825
						.01986915

Table 64. Least-squares equations for body weights in the Spanish line segregating for barring

	$\hat{u}$	$\hat{b}$	$\hat{nb}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	RHS		
								8 week	Housing	Dec.
u	106	58	48	42	24	27	13	6589	350.6	413.4
b		58	0	24	14	16	4	3490	188.5	225.9
nb			48	18	10	11	9	3099	162.1	187.5
h_1				42	0	0	0	2701	146.5	167.6
h_2					24	0	0	1431	75.8	90.3
h_3						27	0	1655	89.3	108.2
h_4							13	802	39.0	47.3

Table 65. Reduced least-squares equations for body weights in the Spanish line segregating for barring

	$\hat{u}$	$\hat{b}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	RHS		
						8 weeks	Housing	Dec.
u	106	10	29	11	14	6589	350.6	413.4
b		106	11	9	10	391	26.4	38.4
h_1			55	13	13	1899	107.5	120.3
h_2				37	13	629	36.8	43.0
h_3					40	853	50.3	60.9

Table 66. Inverse matrix of reduced coefficient matrix of body weight in the Spanish line segregating for barring

	$\hat{u}$	$\hat{b}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$
u	.01122222	-.00027083	-.00523115	-.0007604₂	-.00191281
b		.00983989	-.0011348₇	-.00136915	-.00155137
h_1			.0232504₂	-.00499637	-.0038179₄
h_2				.03223861	-.00824529
h_3					.02997788

Table 67. Least-squares equations for production (periods 1 and 2) and egg weight in the Spanish line segregating for barring

	$\hat{u}$	$\hat{b}$	$\hat{nb}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	$\hat{h}_4$	RHS Period 1	RHS Period 2	RHS E.W.
u	54	25	29	16	12	17	9	565	370	3062
b		25	0	9	5	8	3	272	187	1425
nb			29	7	7	9	6	293	183	1637
h_1				16	0	0	0	177	114	905
h_2					12	0	0	83	74	672
h_3						17	0	219	138	983
h_4							9	86	44	502

Table 68. Reduced least squares equations for production (periods 1 and 2) and egg weight in the Spanish line segregating for barring

	$\hat{u}$	$\hat{b}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$	RHS Period 1	RHS Period 2	RHS E.W.
u	54	-4	7	3	8	565	370	3062
b		54	5	1	2	-21	4	-212
h_1			25	9	9	91	70	403
h_2				21	9	-3	30	170
h_3					26	133	94	481

Table 69. Inverse matrix of the reduced coefficient matrix for production (periods 1 and 2) and egg weight in the Spanish line segregating for barring

	$\hat{u}$	$\hat{b}$	$\hat{h}_1$	$\hat{h}_2$	$\hat{h}_3$
u	.01996016	.0020714 4	-.00459409	.00121842	-.00513243
b		.01909934	-.00445885	.00111179	-.00094794
h_1			.05202644	-.01698239	-.01037408
h_2				.06146689	-.01585890
h_3					.04919431